



Podocarpus [*Nageia*]. 1-3, *P. wallichianus*, cultivated in Ho Chi Minh City, Vietnam, note the flexible leaf and twig apex in contrast to that of *Agathis*; 4, *P. motleyi*, dried specimen from Pasoh Forest, Malaysia.



GYMNOSPERMS

GNETACEAE

NAME: From the genus *Gnetum*, as below.

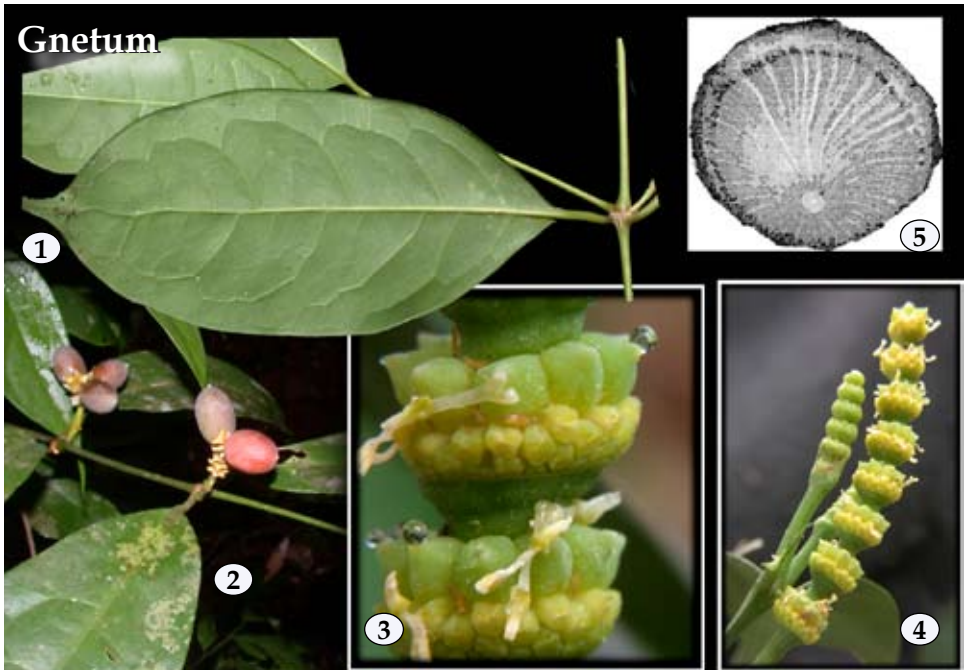
OVERVIEW: About 30 species, all roughly similar species of *Gnetum*, as below, with one species from W New Guinea proposed as a new genus, yet unpublished.

GNETUM. [Derived from a Moluccan name.] 30 species, two in wet tropical Africa, seven species of lianas in tropical S America, and 21 in Asia. In the lowland equatorial forest, the most common appearance of *Gnetum* is as a large liana, dioecious, with a great spike of fruit borne on the lower stem. Only the variable *Gnetum gnemon* is a tree, known in Malay as *melinjau* or *belinjau*. (In 1911, Foxworthy described *Gnetum arboreum* as a tree similar to the liana *G. latifolium* but with small leaves and a tree habit; the collection of 1909 by Robinson was from 900 m in Tayabas, Philippines, and it is not clear that Foxworthy saw the plant. The type specimen and published illustration look as if it were a liana.)

These are gymnosperms but strange members in that the xylem includes vessels and the phloem has companion cells and sieve-tubes (the development distinct from angiosperm sieve tubes), and the broad, thin, and net veined leaf blades look more like angiosperms. The reproductive organs are described as strobili - sexual organs in whorls in spike-like structures, the whorls subtended by fleshy collars. Sometimes described as dioecious but the cultivated trees are evidently monoecious. The female forms a 'pollen drop', a glistening drop at the opening to which pollen sticks. Pollen drawn down micropyle. Male strobili also exude sticky droplets at night, accompanied by stinking odor, visited by nectar-seeking moths of Pyralidae and Geometridae¹. The seed does not form endosperm - a feature that further distinguishes it from the flowering plants; the nature of the double fertilization products is unclear.

In the wet forests of equatorial Asia, this species is typically a single-stemmed tree about two m tall reaching a diameter of no more than two or three cm. However, when cultivated in villages it reach 10-20 cm diameter. When cut transversely, the stem is distinctive in the concentric bands of growth and the clear jelly-like resin that exudes.

¹Kato, M, *et al.* 1995. American Journal of Botany. 82: 862-868.



Gnetum gnemon. 1, opposite leaves with swollen node, and open angiosperm-like venation; 2, fruit of a forest plant in Malaya; 3, fruit of forest plant in Sarawak; 4-5, male flower with glistening pollen drops, from a cultivated tree, Mt. Makiling, Philippines.

The most obvious economic use of *Gnetum* lies in the seeds of *G. gnemon*. In Java more than anywhere else, they are roasted and ground to make the fried chips called *emping melinjo*. Young leaves of many species are eaten fresh or cooked, and commonly show up in Vietnamese salads. The lianas contribute a valued rope,

akar tali in Malay, *akar keliat* in the Philippines. Indeed, the fibers are greatly underexploited. Strong and pliable, they are valued in traditional use and may well represent the best rope in the world. No current taxonomic treatment exists for *Gnetum*, and evidently, we have no regional student of this important family.



GYMNOSPERMS

PINACEAE

NAME: From the genus *Pinus*, as below.

OVERVIEW: The Pinaceae are trees of moderate size with 220 species in 12 genera, and with about half the species in the genus *Pinus*. (For general information, see the website below, and the guide to silviculture of N American conifers^{1,2}.) The pine family includes many of the world's most ecologically and economically important trees. *Pinus*, *Tsuga* and *Abies* form vast forests in the northernmost latitudes. The family is absent from tropical India and Sri Lanka but is well represented in the Himalayan range and adjacent northern areas. Only

Pinus inhabits the core of tropical Asia while at least two genera – *Keteleeria* and *Tsuga* – reach south from their abundant representation in China to northern Vietnam, and *Abies* is probably in subtropical Myanmar.

The family formerly included the bulk of extant gymnosperms, but the current consensus is to recognize a smaller monophyletic group defined as comprising gymnosperms that bear pistillate cones in which the bract-scale complex consists of well-developed scales that are free from the subtending bracts for most of their length, each bract bears two inverted ovules on the adaxial face, and the seed bears a wing that develops from the cone scale. The genera are distinguished critically by further details of bract and seed structure. Most of the trees in the family, and all of our regional species, are monoecious.

PINUS. [Classical Latin name.] An important genus of trees with about 120 species found widely in the Northern Hemisphere with maximum species richness

¹Lovett, R. & M. Frankis. A pine classification. (<http://www.pinetum.org/Lovett>.)

²Burns, R. et al. 1990. Silvics of North America: Conifers. USDA Forest Service.

ness in California and Mexico, absent from tropical S America, India and Africa. In tropical Asia, we find the three-leaf upland pine, *Pinus kesiya*, the two-leaf lowland pine, *P. merkusii*. Vietnam, Laos and Myanmar claim a few additional species including *P. krempfii*, a rare two-leaf pine, possibly basal to the genus.

Pine bark is generally rough, particularly on older trees, peeling in flakes and often of irregular shape. Leaves are linear, a few with minute serrations, and spirally arranged. The cotyledons are whorled. The young seedling bears leaves that are single and spirally arranged; these are soon replaced by the mature condition in which the long-shoots of the twigs bear a spiral arrangement of small brown scale-leaves, each of which bears in its axil a short shoot from which one or more bundles of mature needles are borne; the number and form of needles in each bundle differs among species. The plant body is highly resinous and the foliage is especially pungent. The pollen cones are typically borne on the lowermost branches, numerous, small, papery or fleshy, axillary, cylindrical, subtended by a cluster of overlapping scales similar to the foliage bud. Each microsporophyll is scale-like and bears two inverted pollen sacs abaxially.

Pines should be unmistakable; never confuse them with the angiosperm *Casuarina* (Casuarinaceae). We read too often in the popular literature of Asia of a sea-side pine forest.

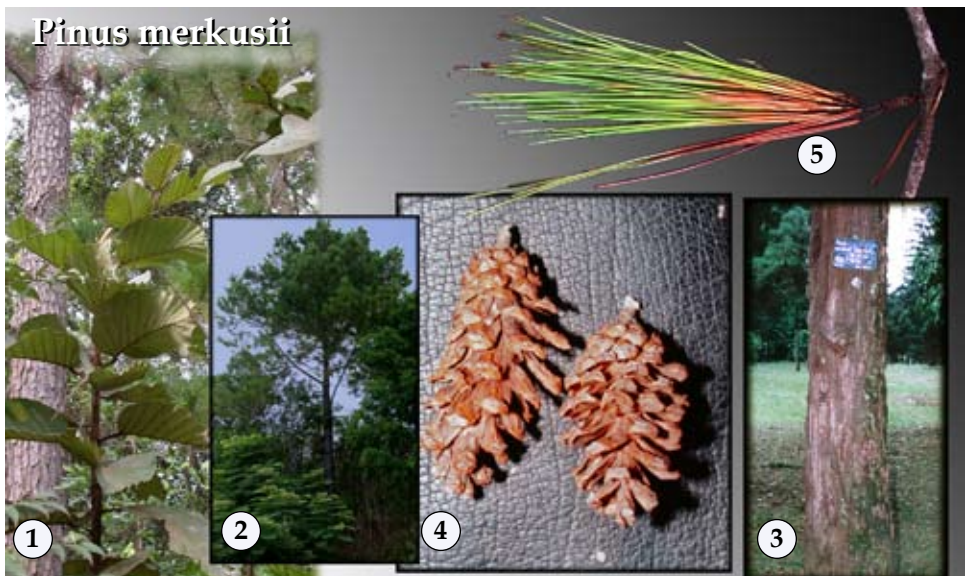
In many books on Asian tropical trees, you will find no mention of the family at all, and you could indeed spend a career in the study of the tropical forest and ignore the pines entirely. For that reason, I perhaps err in emphasis here, but there are good reasons to give the pines some much-needed local publicity. Where the pines are found, they are of immense ecological and eco-

nomic significance; their dominance poses unresolved issues of management that impact upon the economies of three major cities: Chiang Mai in northern Thailand, Dalat in central Vietnam, and Baguio in northern Philippines.

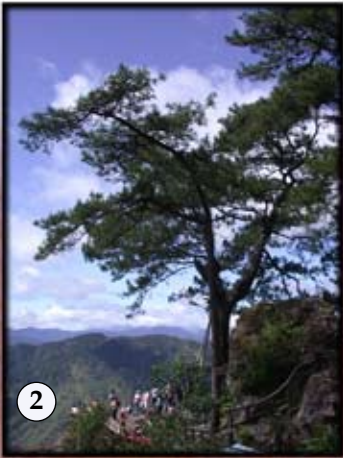
Fossil pine has been found in N Borneo dating prior to the Pliocene suggesting that in drier climates the pines forests may have been more widespread, a conclusion supported in part by allozyme studies that show greater heterogeneity to the east and uniformity to the west. More than a few unanswered questions concern pine ecology: What role is played by fire in the development and maintenance of monospecific pine stands? How do pine trees interact with the broad leaf forest? Were pine forests smaller in historic times? The regional silviculture of pines is equally undeveloped. How best to manage these forests for maximum yield of timber? Can the resin industry be redeveloped? And their are related ecological details still to be uncovered. My ornithological friends tell me that the Red Crossbill (*Loxia curvirostra*), a seed-eating songbird known primarily from high-latitudes, winters in our pine forests where it subsists largely on the seeds of *Pinus kesiya*.

The two-leaf pine, *P. merkusii*, although never a dominant tree, is of equal interest because of the broad ecological and altitudinal range. It has been found at 1000 m in central Vietnam, and growing near sea level in Cambodia in mixed dry dipterocarp forest. It is found as far south as Sumatra and as far east as Palawan and Luzon island.

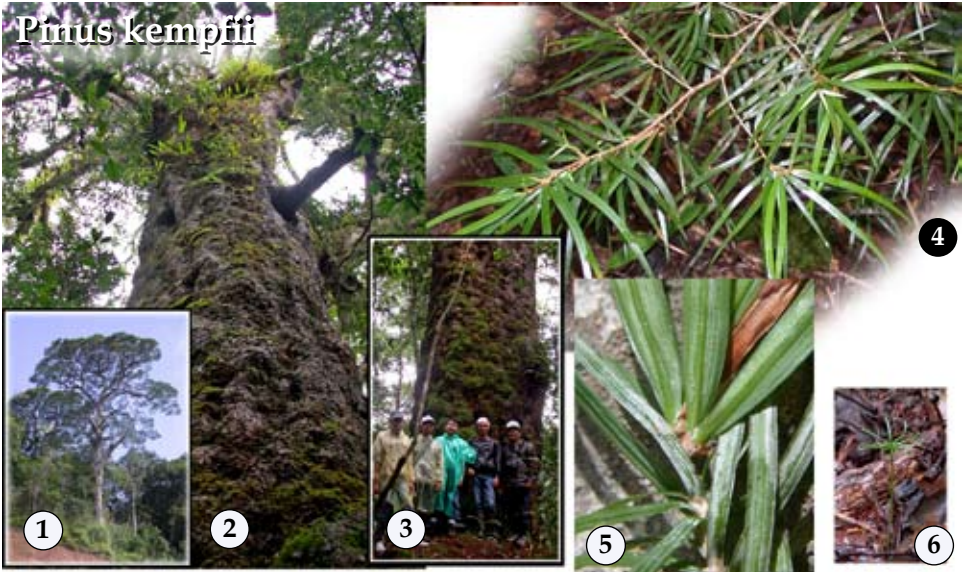
Pinus krempfii is one of the most unusual species of pine. Known only from the Central Highlands of Vietnam between 1200-2000 m, it merits mention on several accounts. First, it is an extremely odd pine in the



Pinus merkusii. 1, in lowland forests of Cambodia, mixed with *Dipterocarpus*; 2, at 800 m elevation in central Vietnam; 3, cultivated in Bogor Botanical Gardens, Java, showing the bark; 4, cone; 5, long needles.



Pinus kesiya. 1-5, Philippines; 1, male cones and needles; 2, mature solitary tree on outcropping at Mines View; 3, sparse open populations in the upper Cordillera, 1700 m; 4, typical bark; 5, timber as used in a century old door, Sagada, Cordillera; 6, thousands of hectares of pine forest in the Central Highlands of Vietnam.



Pinus kempffii, Central Highlands of Vietnam, 1800 m elevation. 1-3, mature trees, showing canopy form and the stout columnar bole of 1.5 m DBH, with a cored age estimate of 900 years; 4, mature leaves; 5, sapling leaves, flattened and in bundles of two; 6, one of many abundant seedlings on the forest floor.

two flat needles per bundle. Molecular evidence rejects the suggestion that it be removed to its own genus^{4,5}. It is certainly a pine, perhaps basal to the genus and most closely allied with the white pines. Second, the ecology differs from *P. kesiya* in that it lives in mixed composition with broadleaves, and also in that the seedlings regenerate within the forest and gap edges rather than

invading open ground. A final reason to note this species is simply that it is one of the more magnificent trees in Asia. Although not especially tall, attaining perhaps no more than 30 m, in these high mountains it easily emerges above its neighbors with a great hemispherical crown. The clear straight trunk exceeds two m DBH in the largest individuals, and while it may not be especially old - studies of growth rings suggests an age of 750-900 years for the largest trees - the damp mountain habitat and the rugged moss-covered bark creates the visage of an ancient relic.

³Myburg H, *et al.* 1997. *Silvae Genetica*. 46: 295-301.

⁴Wang, X, *et al.* 2000. *Plant Systematics and Evolution*. 220: 21-36.

⁵Brodrribb, T, *et al.* 2008. *New Phytologist*. 178: 201-209.



MAGNOLIIDS: AUSTROBAILEYALES

ILLICIACEAE

NAME: From the genus *Illicium*, as below. Popularly known as the star-anise family, from the commercial spice.

OVERVIEW: Only the genus *Illicium*; molecular evidence removes these plants from proximity to the Magnolias and aligns them with the monotypic *Austrobailleya scandens*, a liana of NE Australia, and draws them close to the herbaceous lotus of the order Nymphaeales.

ILLICIUM. [Latin, allurements, in reference to the spicy odor.] An isolated genus of 42 species; five in E. North America and Mexico and maybe 32 in E. Asia, from southern Japan to Sumatra and from Assam to the

Philippines, with a center of species numbers in northern Myanmar and Yunnan. We find maybe 20 species in tropical Asia, scattered, with locally differentiated species in each mountain region, two on Kinabalu, three in Malaya, and just one in the Philippines. The Malay name is *bunga-lawang*.

These are small tree and multi-branched shrubs, rarely exceeding 10 cm DBH. The leaves are entire, spirally clustered from short leaf stalks without stipules. The flower bears a colorful corolla of numerous parts in several whorls, free and overlapping. The stamens are numerous, spirally arranged on a receptacle whereas the mostly five carpels form a single whorl, each carpel one locular, each locule with one ovule, nearly basal. The fruit forms a star-like follicle, each carpel splits along the upper side and squeezes out a single shiny seed.

Illicium bears a general if superficial similarity to the Annonaceae and to the Magnolias. They differ from



1-2, *Illicium philippinense*, leaves in spiral, upturned clusters, star-anise fruit, about 15 cm across; 2, flower, about 2 cm across; 3, *Illicium cf. griffithii*, 1800 m, Vietnam, fallen fruit about 2.5 cm across; 4, floral drawing *Illicium verum*. ((1-2 © Leonardo L. Co) 4, from BAILLON *loc. cit.*).

Magnolias in the absence of a stipule and the carpels are arranged in a single whorl. From the Annonaceae they lack the net-like fibers beneath the twig bark, the leaves are in tight spiral clusters.

The flowers of some North American species are pollinated by Diptera; others may be pollinated by beetles. However, the bulk of the Asian species have never been examined. The highly distinctive fruits are fleshy at first, and although it is common to find them in mountain forests scattered on the ground, I have seen no evidence that animals take them. Many are reputed to be strong poisons. The seeds are dispersed ballistically, and like so many trees with that dispersal mode, they can form exceedingly dense local populations.

Some are popularly cultivated for the flowers and fruit. *Illicium verum*, the star-anise of commerce is historically grown in southern China, but now Vietnam is developing its own industry. The strong licorice odor comes from anethole, the same chemical constituent as the European *Pimpinella* (Apiaceae), used since antiquity for the flavor of licorice. Star-anise is one of the fundamental flavors of Indian dishes like *garam masala*, and also Chinese five-spice powder. It is used to produce shikimic acid, which in turn is the base chemical for an effective anti-flu medicine. This led to a short-lived boom in *Illicium* plantations, followed by a bust when, in 2005, alternative production techniques reduced the need for the natural source.



MAGNOLIIDS: CHLORANTHALES

CHLORANTHACEAE

NAME: From the genus *Chloranthus*, as below. No vernacular family name applies, although individual species are well known and readily named.

OVERVIEW: A small family in its own order, the Chloranthales, a status that is merited by both morphology and molecular data, which are singular and have defied an easy placement, although it is clearly linked to

the basal angiosperms. The family comprises four genera and about 65 species¹, pantropical but the genera differ in their richness and abundance among the different continents. All four genera are found in tropical Asia, but only a few species of each, and none are large trees. *Hedyosmum* alone occurs in tropical America, but there it is species-rich, diverse and abundant, with several species reaching large diameters. Africa is without a family representative, and only an odd *Ascarina* is found in Madagascar. The cited molecular study found that *Hedyosmum*

¹Zhang, L. *et al.* 2003. International Journal of Plant Science. 164: 383-392.

Chloranthaceae



Chloranthaceae. 1, *Chloranthus spicatus*, floral diagram from BAILLON *loc. cit.*; 2-6, *C. erectus*, Philippines; 2, in flower; 3, the widened node with scar and odd stipule-like teeth; 4, toothed leaf margin; 5, flower with a fertile anther; 6, in fruit; 7, *Sarcandra glabra*, fruit, toothed leaf margin, (2, 6 © Leonardo L. Co; 7, © Nestor Bartolome.)

is sister to the other genera, followed by *Ascarina* and *Chloranthus* + *Sarcandra*.

All are evergreen woody plants, trees and treelets, with unspecialized vessels or lacking vessels (*Sarcandra*), with

opposite leaves and toothed margins and leaf bases that join across a swollen node with a type of stipular flange. The leaves are aromatic. The genera differ in unisexual versus bisexual flowers, and in the presence and arrangement of the floral organs. Flowers and inflorescence are highly reduced and open to various interpretations.

In tropical Asia, these odd plants are rarely recognized in the field where they are often overlooked or dismissed as small Rubiaceae - look for the toothed margin - or Rhizophoraceae, or sometimes misidentified as a *Gnetum* because of the small flowers in the spikes and the swollen flattened nodes.

☞ - Unisexual Flowers - ☞

HEDYOSMUM. [Greek, fragrant, from the leaves.] A genus of 35-40 species, chiefly Neotropical, where it is often



Chloranthus indicus (left) and *Sarcandra chloranthoidea* (right), adapted from WIGHT *loc. cit.*

fairly common in cloud forests, with a few species at low elevations, and including a few medium-sized trees. In Asia, only one small treelet, *H. orientale*, with a scattered distribution including Hainan and Vietnam, Sumatra and Borneo, and probably uncollected in other wet hill forests over 1000 m. It is certainly a tree easy to overlook. The male inflorescence is an odd cone-like structure, each flower bearing numerous stamens. (Not illustrated.)

ASCARINA. [Latin for worm in reference to the shape of the anthers.] *Ascarina* includes 12 species, chiefly in the Pacific Islands with one species reaching as far west as North Borneo and the Philippines, and then with an outlying representative in Madagascar. *Ascarina philippinensis* is a small tree, usually less than two m tall, often encountered in lower montane forests. The floral biology of the genus needs field observation, particularly regarding the distribution of sexes. (Not illustrated.)

CHLORANTHUS. [Greek, green flowers.] *Chloranthus* is represented by 18 species found from Japan south to New Guinea and west to India and Sri Lanka, with maybe six species in tropical Asia. All are small trees, rarely exceeding one cm DBH. *Chloranthus erectus* is conspicuous when bearing mature white fruit. *Chloranthus spicatus*, native to China, is cultivated in scattered places, especially in Java.

SARCANDRA. [Greek, fleshy anthers.] Only two species, *Sarcandra chloranthoides* of India and Sri Lanka and *S. glabra* from NE India to China and Korea south to the equator in montane habitats as far east as New Guinea. These two species are similar to *Chloranthus*, equally small in stature, but bearing red fruit, and completely lacking vessels. Sterile material is especially close to *C. erectus*, but *Sarcandra* typically dries red-brown instead of green-gray. The flowers of each spike open slowly over several days. The anthers dehisce a day or so after the stigmas are receptive. The flowers are fragrant.



MAGNOLIALES

The modern view of this order, following APG III and STEVENS *loc. cit.*, begins with three families traditionally associated with one another - Magnoliaceae, Annonaceae and Myristicaceae - and adds to them three small families for a total of 154 genera and 2929 species. Magnolias are of minor ecological importance in tropical Asia whereas the Annonaceae and Myristicaceae are among the most important of families.

Strict synapomorphies of the order are molecular or otherwise cryptic in nature. (Molecular studies related to the order are cited under each family, the phylogeny below follows STEVENS *loc. cit.*) We can characterize the order as woody plants bearing spirally or alternately arranged broad elliptic leaf blades with pinnate nerves (except *Liriodendron*) and an untoothed margin. A few floral and ecological features are widespread within the order. Most of the species of the Magnoliales are thought to be beetle-pollinated, while at least in the Magnolias and some Annonaceae the flowers heat at night. The seed is large, and wide dispersal is achieved chiefly by vertebrates. The leaf blade includes one type or another of ethereal oils, typically in dots glands that give these plants a particular odor. The trees of our region are entirely shade-loving plants of the forest without weedy representatives.

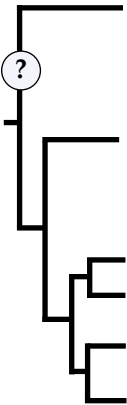
While those noted feature characterize the order as a whole, each of the three major families appears distinct,

but each in its own way with notable differences and combinations of similarities among the three. Plants in the order are exclusively trees except the Annonaceae which are rich in lianas. Annonaceae and Myristicaceae have a short unswollen and exstipulate leaf stalk, while that of Magnoliaceae is entirely different being tapered from base to apex or even somewhat swollen at the base where it often fuses with the well-developed encircling stipule. The families all lack any noticeable exudate except Myristicaceae where it is strong and bright red. Each family is distinct with regard to branching and leaf arrangement: the Magnoliaceae bear spirally arranged leaves with lateral branches that include short and long internodes; in the Annonaceae the upright shoot bears spirally arranged leaves with uniform internodes and lateral branches with distichous leaves, or alternatively in the case of the lianas, *Goniotalamus* and some Neotropical trees, the upright stem has a distichous arrangement as well. In contrast, the upright stem of the Myristicaceae bears spirally arranged leaves but with combinations of short and long internodes creating a pagoda branching pattern. All families typically bear bisexual flowers except Myristicaceae, which are typically unisexual-dioecious. Annonaceae and Myristicaceae are chiefly of the lowland equatorial forests while Magnoliaceae are chiefly in the subtropics and also reach well into the northern Temperate Zone.

Such contrasting features among these basal families of the angiosperms raise numerous issues that impinge upon our understanding of how flowering plants evolved. How did the ‘stipule’ of Magnolias arise? Does it relate in any way to stipules in other angiosperms? By what changes could the small and strange unisexual

flowers of Myristicaceae and the large bisexual flowers of Magnolias evolve from a common ancestor? If Myristicaceae are sister to the other families, then why are fossil nutmegs so recent (no earlier than Miocene, some 10-20 million years ago) and why is the molecular divergence among the nutmegs so modest?

Phylogeny of Magnoliales

	Family	General Description	Trees of Tropical Asia
	Myristicaceae	20/500, pantropical, different genera in different continents, trees, red exudate, leaf exstipulate with short simple leaf stalk, unisexual flowers, dioecious, single-seeded arillate fruit.	5/300, species-rich and abundant especially wet equatorial lowlands.
	Magnoliaceae	2/222, Asian-American, no exudate, conical encircling stipule, leaf stalk basally swollen or tapered toward the blade, often joined to well-developed encircling stipule, bisexual flower.	1/20, diversity of form increases toward China, consistent in equatorial lowlands but at low abundance, locally abundant - especially seasonal and lower montane.
	Degeneriaceae	1/2, Fiji.	0.
	Himantandraceae	Monogeneric, <i>Galbulimima</i> , tropical Australia, Asian.	2, from Sulawesi, New Guinea, Australia.
	Eupomatiaceae	1/3, small trees and herbs, New Guinea to E Australia.	0.
	Annonaceae	129/2200, different genera in different continents (except <i>Anaxagorea</i> , <i>Xylopia</i> , <i>Popowia</i>) no exudate, leaf exstipulate with simple leaf stalk, bisexual flowers, multiple carpels.	32/860, species-rich and exceedingly abundant trees and lianas in most forests below 800 m; not mangrove, poor in secondary forests.



MAGNOLIIDS: MAGNOLIALES

MYRISTICACEAE

NAME: From the genus *Myristica*, as below. In English these trees constitute the *nutmeg* family, from the seed of commerce, the name of which is likely a corruption of *nois-muscade* or musk-nut. A few individual species are distinguished with local names, especially in those peripheral locations with only a few indigenous species. However, in general, vernacular names apply to the family as a whole and are mostly based on some derivation of *darah*, blood, in reference to the characteristic red exudates: *chendaraban*, *penaraban* and *darah-darah* (Malay, generally), *kumpang* (Iban), *duguan* widely in Philip-pines, but some *Knema* as *tambalau*.

OVERVIEW: The wild nutmegs form a cohesive and easily recognized family of roughly 20 genera and 500 species with five genera and maybe 300 species in tropi-

cal Asia. The family as a whole is strongly monophy-letic^{1,2}. In distribution, the nutmegs are pantropical but with different genera in the different continents. The in-dividual Asian genera appear to be clearly monophyletic, but the Asian taxa as a whole may or may not form a clade. There is modest evidence that independent clades diverged in America, Africa and Asia at an early age. However, the low molecular divergence among extant lineages and fossil evidence indicating a Miocene origin contradicts that scenario.

Within Asia, the center of diversity lies in Borneo, and yet the genera differ greatly in details of distribution. *Myristica* is most species-rich in New Guinea and dimin-ishes to the west, whereas *Knema* is richest in the Malay Peninsula and the wet parts of Borneo and has only a single species in New Guinea.

The nutmegs are medium-sized evergreen dioecious trees (*Endocomia* is monoecious) with tiered branching, alternate simple entire leaves lacking stipules and bear-ing a bitter red sap and a distinctive single-seeded red arillate fruit.

In stature, the Myristicaceae are exclusively woody, perennial upright trees. The range of stature is great: *Myristica gigantea* may reach 45 m in height while some

¹Sauquet, H. *et al.* 2003. Botanical Journal of the Linnean Soci-ety. 142: 125–186.
²Doyle, J. *et al.* 2004. International Journal of Plant Science. 165: 55–67.

species of *Knema* reproduce at a height of one m. The majority are trees of about 10 m height. Multi-branched shrubs are not known, neither are herbs or soft perennials. In contrast to the Annonaceae, there are no lianas. Plank buttresses are not common but prominent stilt roots are present in those few species that prefer swampy land.

The larger trees form a straight mast-like trunk with a lollipop or pyramidal crown of dense foliage. The red exudate (*kino*) from the trunk and twigs is characteristic of the family, but varies in amount, clarity and tint among different species. Sometimes it is bright and clear, copious and gushing out, in other species it is meager and almost milky pink. The freshly cut wood is white, turning yellowish brown, and stained by the *kino*; it is soft and light to moderately hard and heavy with very narrow rays. The heart-wood is darker in color often dark red or purplish brown and is heavier, harder and more durable.

The nutmeg bark is often diagnostic to species but is less consistent among genera. In some species the bark is as black as *Diospyros*. In many *Myristica* it is brittle, coal-black or grayish-black, but some species bear a brownish bark. That of *Horsfieldia* is brown or grayish brown, *Knema* gray, greenish-gray or less often a brown-gray while in *Gymnacranthera* it is reddish brown.

The upright stem grows in flushes with a series of elongate branchless internodes interrupted by a flush of spirally arranged leaves that bear axillary branches like spokes in a wagon-wheel, similar to *Diospyros* (Ebenaceae). The lateral branches bear leaves that are more or less alternate and all of the same size. A few species, e.g., *Horsfieldia succosa*, have spirally arranged leaves more or less clustered toward the tips.

The twig tips are often recognizable to family from the covering of red hairs (simple or stellate) or red granules represented in ways that diagnose individual species.

Twig characters are diagnostic for species, especially so in *Knema* in which the twigs vary in thickness (two cm to very slender), in color (red, gray, black to straw) and in the presence of hairs. Lenticels are found in all genera except *Endocomia*. In a few species of *Myristica*, the bark of the twigs cracks in small squarish flakes. A few species of *Horsfieldia* (and a few species of *Myristica* in New Guinea) have two lines or ridges on each side of the twig, stretching from one leaf base to the next. In *Horsfieldia wallichii*, the twigs are often hollow, while some species east of Borneo have ants in the twigs.

The leaf blade often has a faint spicy odor. Only rarely are tiny bright dot glands visible when the blade is held to the light. In the majority of species, the leaf stalk is about 7-12 mm long, fleshy and terete, without swellings and without stipules. It can be relatively long and sinuous in most *Myristica* and in *Knema curtisii*, and very short in *Horsfieldia sylvestris* and slightly winged in *H. succosa*.

The leaf blade ranges in size from 80 cm long in juveniles of *Knema hookeriana* to four or five cm in *K. curtisii*. The leaf-base may be acute or rounded or rarely cordate, chiefly leathery, rarely flimsy or delicate. The

color of fresh and dry leaves is roughly diagnostic for species, and to some extent, genera. In many species of *Myristica*, most species of *Knema* and some species of *Gymnacranthera* the undersurface of the leaf is glaucous or even white with a waxy bloom. Reddish or coppery undersurface is found in *Gymnacranthera bancana*, *Horsfieldia crassifolia*, and *Myristica cinnamomea*. The lower surface is sometimes punctate, the best example being *Horsfieldia punctatifolia*, where it is visibly covered with black dots.

The midrib is distinct and often stout and raised above in all of our genera except *Gymnacranthera* in which it is sunken as a sharp channel. The nerves are usually raised on the upper surface, but in *Myristica* (and *Knema laurina*, *H. wallichii*, *H. reticulata*) the nerves are sunken, the intervening panels billowed or even blistered, especially in the fallen leaves.

The inflorescence is fundamentally a multi-branched panicle and fundamentally axillary from either new leaves or at older nodes where the attendant leaf has fallen. The inflorescence branches are typically subtended by small bracts and two genera (*Knema* and *Myristica*) bear a bracteole on the pedicel beneath each flower. The position of the bracteoles on the flower stalk in *Knema* is often diagnostic to species.

Myristicaceae are strictly dioecious except in monoeocious *Endocomia* although sex changes from male to female are known in cultivated trees. The perianth is

FIELD RECOGNITION: MYRISTICACEAE

Wagon-wheel branching.

Mature tree with a straight, mast-like trunks, the lollipop or pyramidal crown of dense foliage.

Stilt roots are present in swamp species. red exudate (faint pink to bloody) at twig break and slash.

Characteristic terminal bud: a single pre-formed leaf covers the apex, covered in long red hairs or red granular excretions.

The leaves of lateral branches alternate in a plane, of equal size, nerves strong, veins often inconspicuous.

Blade often with faint spicy odor, often with oil glands sometimes visible as bright dots when backlit.

The leaf stalk short, uniform, without swelling, without stipules.

Dioecious, small flowers with 3-part perianth, typically clustered on branches (look for old scars and clusters).

Characteristic arillate fruit.

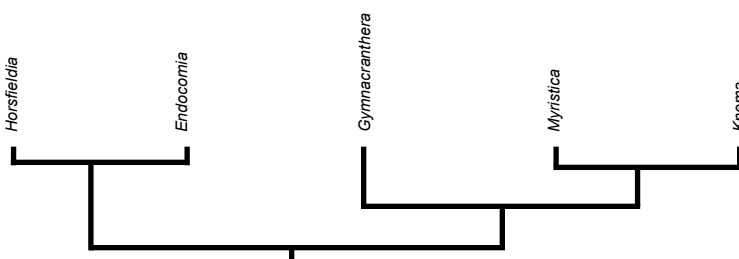















FIELD CONFUSION

Other trees with red exudate, such as *Pterocarpus* and *Macaranga*, would never be confused with nutmegs.

Annonaceae are similar in leaf form but lack exudate and the twig bark peels to display fishnet fibers

Lauraceae are similar in leaf form, but with a leaf stalk thickened near the twig, without wagon-wheel branching, and mostly without red hairy apex.

Diospyros with similar branching, and some nutmegs with very black scaly bark, but ebonies bear no exudate, and have leaves of different sizes that usually bear thick yellow or black leaf glands; the apex usually glabrous or silvery scaly, not red hairy.

GENUS	NOTES		
<div><p><i>Horsfieldia</i></p><p><i>Endocomia</i></p><p><i>Gymnacranthera</i></p><p><i>Myristica</i></p><p><i>Knema</i></p></div>	  	<p>180 species, frequent, abundant, distribution as wide as the family in Asia; flower stalk without bracteole, flower typically with 2-part perianth, floral parts glabrous, vegetative parts reddish or red hairy, twig lenticellate, blade fragile, dries with parchment-like texture, midrib raised above, nerves raised (or sunken blistered), often looped near the margins, lower surface green (fresh) drying red.</p>	
	  	<p>4 closely related species; scattered, low abundance; distribution and appearance similar to <i>Horsfieldia</i>, but evidently monoecious, trunk with white-to pinkish exudate, twigs without lenticels, floral perianth hairy within, possibly nested within <i>Horsfieldia</i>.</p>	
	  	<p>20 species, frequent, abundant; Malaya and Sumatra, Borneo, to New Guinea, east coast of Luzon; flower stalk with bracteole, fruit small, aril deeply cut to base; blade glaucous below, nerves darker and looped, midrib deeply channelled above.</p>	
	  	<p>175 species, frequent, low abundance, mostly medium to large trees, distribution equal to the family in Asia, many local endemics, with greatest richness in New Guinea; flower stalk with bracteole, aril deeply cut, twig stout, ridged or flaky, lenticellate, blade green below, dries blackish-gray, nerves typically looped near the margin and deeply sunken above.</p>	
	  	<p>85 species, frequent, abundant, many widespread species, many small statured. India (not Sri Lanka) and S China to New Guinea, especially Borneo and the Malay Peninsula; flower stalk with bracteole; bud, flower, fruit with red granular excretions or hairs, twig often ridged, lined, flaky, lenticellate; blade firm, leathery, persistent, with raised midrib and fish bone nerves, (<i>K. laurina</i> sunken above) whitish glaucous below.</p>	

Phylogeny of Myristicaceae, the trees of tropical Asia are shown as a provisionally monophyletic clade (weak support), with strong support for *Knema* and *Myristica* as sister taxa, and moderate support for the rest of the structure; following Sauquet *et al.* as cited in the family introduction; floral drawings adapted from Warburg *loc. cit.*

fleshy, typically in three parts, and valvate. The form of the anthers varies diagnostically among genera. In general, there are three to 30 exclusively fertile stamens, the filaments united as a column, the extrorse anthers with longitudinal slits. Unlike the androecium, the gynoecium is remarkably uniform and that uniformity was the basis for 19th Century practice of regarding the family as a single genus. The female flowers bear a single unclosed carpel with one nearly basal ovule. The mature fruit varies diagnostically to species in size and color from red to yellow. Many species in Asia bear a tomentum, especially the granular coating that characterizes *Knema*, and the remarkable woolly coat in *Myristica villosa*, but differences in the fruit among genera lie chiefly in whether the aril is entire and covers the seed or partially cut and lobed at the tip or fully lacinate to the base.

The endosperm or albumen is hard and nearly always contains fat and a fixed oil. Starch is abundant in the endosperm in *Knema*, and at least in some *Myristica* (but see the illustration) and generally absent from *Gymnocranthera* and *Horsfieldia*. The endosperm is ruminate in all genera in Asia (not so in some American genera).

The nutmegs are important members of the lowland equatorial wet forests where you might encounter 30 to 40 species within a km or so, representing about 4% of total tree species and a similar fraction of the trees. In general, species of nutmegs are widely and uniformly distributed within their geographic range. As one example, about 60% of all the Malayan species of nutmegs could be found in 50-ha of Pasoh Forest in the South Central part of the Peninsula.

If the nutmegs share many vegetative features with the Annonaceae, it must be remembered that nutmegs are a much smaller family with only a tenth of the number of species, and display a far greater uniformity. With regard to diversity and distribution they more closely parallel the persimmons (*Diospyros*), with about the same number of species, both locally and regionally, a similar abundance, and with a comparable level of vegetative homogeneity.

Asian nutmegs are generally intolerant of very dry conditions and of fire. We have no real equivalent to those species of *Virola* that thrive in the dry savannahs on the Atlantic coast of Brazil. Consequently, species richness falls rapidly as we move north from the equator and especially so in the strongly seasonal lands of continental Asia and western Philippines. Only a few nutmegs are mountain plants that grow above 1000 meters: *Horsfieldia glabra*, *H. subalpina*, and *Knema rigidifolia*. Within the lowland forest, species are chiefly distributed along gradients of moisture and topography.

The flowers are generally fragrant at night and presumed to be beetle pollinated although there is much in the flowers that contrasts with the more typical beetle pollinated flowers of, for example, the magnolias. No one knows if these flowers heat at night as is the habit of some Magnolias and some Annonaceae, but we might suspect heat production in the larger flowers of say *Knema hookeriana*. Nothing demonstrates the poverty of our knowledge so much as to note that the cultivated nut-

meg, *Myristica fragrans* - the tree that launched the European conquest of Asia - was demonstrated to be beetle pollinated only in the 1980s. Similarly, even though the nutmeg has become the principle crop of the Caribbean nation of Grenada, the identity of pollinators on that island remains unknown. The only significant study of pollination of nutmegs in Asia is for *Myristica insipida* in the geographically eccentric site of Queensland, Australia³. It is worth noting the results at length. The trees bloom at night, males for one night, females receptive for two or three days. A vast number of thrips were found but no evidence that they carry pollen. Nine unnamed and likely new species of beetles - representing five families - made up most of the effective visitors and were found to carry pollen. Visits to female trees were seen but evidently without reward or even without effective entry since the stigma protrudes through the narrow opening of the petals. *Knema*, with flowers tomentose outside and often bright red within, may be similar, and yet the anthers present their scant pollen in such a distinct manner that we may suspect a novel function. *Horsfieldia*, with their tiny yellow perianth will likely also to be found variant in a specialized way. *Horsfieldia* are certainly the strongest scented of the nutmegs.

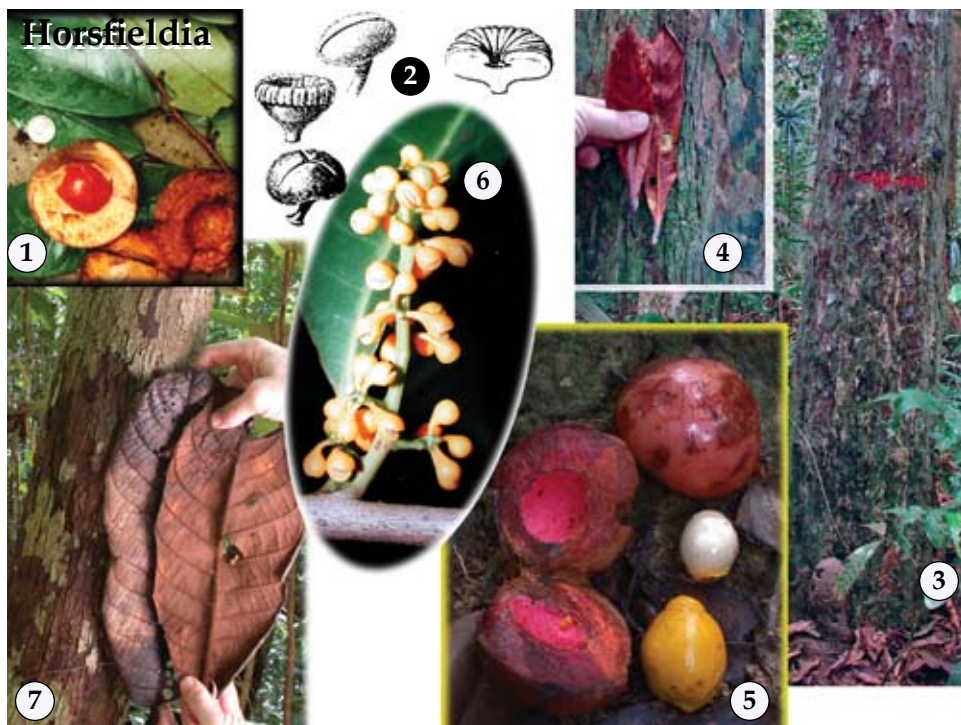
It takes little imagination to see that the single seed exposed by the split shell and covered in a red fleshy aril is attractive to birds. To say that these trees are dispersed by toucans in America and hornbills in Asia is true, and yet that is too broad a generalization. Pigeons and doves may be more effective dispersers for the small-fruited species of the understory while small mammals may play an important role in secondary dispersal. Scatter hoarding of the stripped seeds may be an important element in local dispersal. The largest fruit, which are nearly the size of a small apple, may differ as well in that they seem no more than tardily dehiscent and can be found on the forest floor with a bite taken out of the side. The seeds of *Horsfieldia irya*, *H. wallichii* and *M. elliptica* float in water. At least in *H. irya* the seeds have hollow spots in the endosperm.

Other than the nutmeg of commerce, the family has been little studied and hardly utilized at all. The wood is thought indurated, subject to fungi, termites and powder-post beetles, and easily split. Nevertheless, it is attractive with tight grain. Those species of *Myristica* and *Horsfieldia* that take a fine finish are underappreciated as furniture wood.

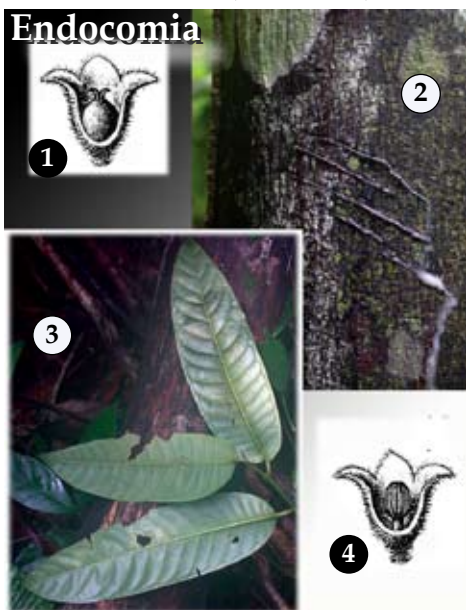
A prospective student of the family will find that the species' taxonomy is unusually well-described and organized in a wealth of published papers. Three students of the family have produced over a thousand pages of literature. The recent taxonomic account in *Flora Malesiana* summarizes several decades of research and publication by W. J. de Wilde based in Leiden, and the text includes reference to his many monographic treatments for Asian and other genera⁴. James Sinclair, working out

³Armstrong, J. 1997. American Journal of Botany. 84: 1266-1274.

⁴de Wilde, W. 2000. Flora Malesiana. 14: 1-634.



Horsfieldia. 1, *H. gracilis*, Lambir, Sarawak, fruit is thick walled the red aril covers the seed; 2, flower and androecium (adapted from Warburg *loc. cit.*); 3-5, *H. sucosa*, Pasoh, Malaya; 3-4, bole and fallen leaves, red, thin, fragile; 5, fallen fruit of same, thick walled, globose, glabrous, here with yellow aril; 6, small inflorescence, more typically branched panicle, two-part perianth spreading, each flower ca. 3 mm wide; 7, *H. reticulata*, Lambir, Sarawak, fallen leaves, red, fragile, sometimes nerves sunken above, and bark reddish, cracked.



Endocomia. 1 & 4, female and male flower, about 5 mm long; 2, tree, 10 cm DBH, blackish bark, milky with a tint of pink, unusual for the family; 3, leaf about 20 cm long, glabrous, green twigs, a bit like *Horsfieldia*. (Drawing from Warburg *loc. cit.*)

of Singapore in the 1950s and 60s, provided highly detailed descriptions of the Malayan and Bornean species⁵. And Warburg's 19th century monograph is still a useful description of species although it should be read in consultation with the current treatments⁶.

The nutmeg family has many advantages for the student in the field: these trees are relatively abundant, they flower frequently, make excellent specimens, are well-described in literature, and most species are easily recognized. They hold great ecological and phylogenetic interest while remaining greatly underexploited economically. The nutmegs are very much in need of a student resident in Asia to study the living trees.

HORSFIELDIA. [Commemorates Thomas Horsfield, d. 1859, American from Bethlehem, Pennsylvania, visited Java in 1800 as a ships doctor and returned to spend nearly two decades collecting plants and animals in Java and Sumatra, author of '*The natural history of Java*', etc.] Maybe 180 species, from Sri Lanka, India, Myanmar and Thailand to Vietnam, S China to Hainan, Malay Peninsula, and with less richness eastward to N. Australia and Polynesia. The distribution is centered in

⁵Sinclair, J. 1958. Gardens' Bulletin Singapore. 16:205-472.

⁶Warburg, O. 1897. Nova Acta Academiae Caesaricae Leopoldino-Carolinae Germanicae Naturae Curiosorum. 68: 1-680.

the Malay Peninsula with 25 listed species, many shared with a secondary center in Borneo, and a different group of perhaps 30 species in New Guinea.

Medium to big trees often with a rich red brown flaky or fissured bark. The leaf stalk is short and stout. Twigs striate, sometimes lenticellate, rarely (e.g., *H. brachiata*) with two raised ridges extending along the internodes. The midrib and nerves are usually raised above and obviously looped near the margin. In *H. wallichii* the large coarse leaves are almost blistered on the upper surface. Perhaps a majority of species have a persistent red indumentum on the lower leaf surface, and the blade often dries a shade of red. The lower surface is never white, and the blade is usually much thinner than in *Knema*. For most species, the leaf texture is very thin and fragile, parchment-like and they rot away very quickly. The inflorescence in *Horsfieldia* is often large, an open lax panicle, the flowers tiny and waxy-yellow. The perianth is typically reduced to two members that only weakly spread apart envelope-like. Although the flowers are among the smallest of the family, the mature fruit can be exceedingly large. They are nearly always globose and glabrous, the pericarp leathery or juicy succulent. The

aril completely covers the seed. Starch is absent in the endosperm.

ENDOCOMIA. [Greek, in reference to the hairs within the petals.] Maybe four species, evidently all closely related. They might be more common than the number of collections indicate because in the field they can be overlooked as *Horsfieldia brachiata*, especially when sterile. The bark is dark, sometimes nearly black while the exudate in *Endocomia* is nearly milky. The twigs are terete and without lenticels. The inflorescence is an open branched panicle also much like *Horsfieldia* but the tree is evidently always monoecious. However, there is much uncertainty about the distribution of sexes within the inflorescence or among trees. The flowers also differ from *Horsfieldia* in that the petals spread at anthesis and the inside of the petals are uniquely hairy. Field studies of reproduction are desirable. These trees seem to be always in sparse abundance, typically as a few scattered large trees. It is possible that these few species are monophyletic as a group and yet nested within the great breadth of *Horsfieldia* and molecular studies are needed.



Gymnacranthera. 1-3 bark diversity and fallen leaves; 1, *G. forbesii*; 2, *G. bancana*; 3, *G. farquhariana*; 4, fresh leaves of *G. forbesii*, glaucous below with looped dark nerves, sunken midrib above, and open branched inflorescence of small yellow flowers; 5, detail of dry blade with sunken midrib; 6, drawing of the fruit adapted from Warburg *loc. cit.*

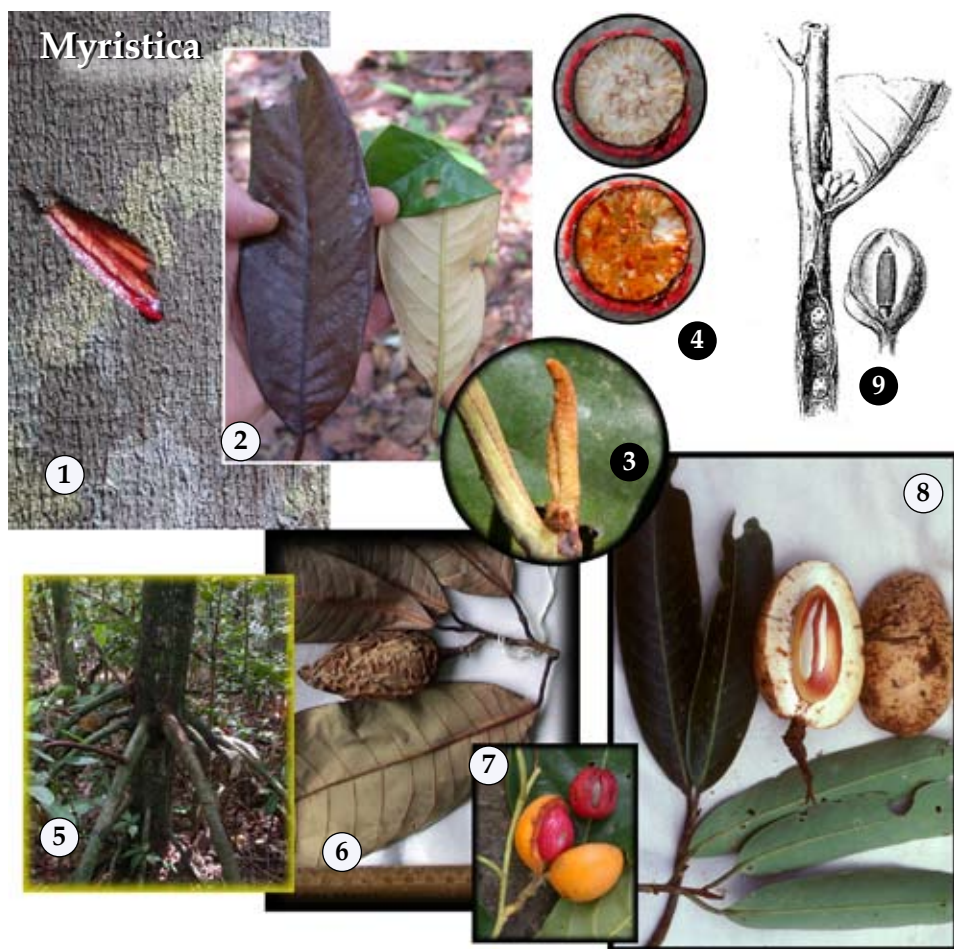
GYMNACRANTHERA. [Greek for naked pointed anther.] About 20 species from Southern India to southern Thailand, the Malay Peninsula and eastward to Borneo, the Philippines and New Guinea, with richness centered in Borneo.

The genus is similar to *Myristica* in the fruit which bears a deeply laciniate aril, in the open branched panicle and in the flower, although here there is no bracteole on the flower stalk. The leaf is similar to *Knema* in the glaucous lower surface, but the nerves are obviously looped near the margins and colored blue or green against the pale background, whereas the veins are not usually visible, and here the midrib on the upper surface is channeled. That last feature provides the most obvious diagnostic feature in the field to distinguish *Gymnacranthera* from other Asian genera in the family.

The individual species differ in bark characters, in the thickness of the leaves, the number of nerves, wheth-

er these are raised or level with the leaf surface, and in the shape of the fruit. The flower is relatively uniform among species. Included here are several common if not constant elements in the lowland forest, especially the widespread and abundant *G. forbesii*. Also notable is the highly distinctive *G. bancana*, the lower leaf surface of which bears dense reddish hairs that makes the canopy appear black when seen from below. In ecology, the most abundant species, *G. forbesii*, seems to prefer wet ground.

MYRISTICA. [Greek, a sweet juice.] 175 species from S India, Sri Lanka, Myanmar, Thailand, Indochina, Malay Peninsula to N. Australia and Polynesia; a single species in S China, the endemic *Myristica yunnanensis*. *Myristica* differs from the other Malayan genera in the structure of its androecium which is a stalked column to which the eight to 30 linear anthers are completely



Myristica. 1, blackish bark, bright red exudate; 2, fresh and fallen leaves, raised midrib and weakly sunken nerves, some spp. golden-copper below; 3, twig apex; 4 XS of seed (same as 7) natural and stained with iodine; cf. *Knema*; 5, black bark and stilt roots typical of the genus in swampy ground; 6, typical herbarium specimen, wrinkled oblong pointed fruit, long leaf stalk, blade pale below, deeply sunken nerves above; 7 & 8, fresh leaf and fruit, thick walled and deeply cut aril; 9, androecium, and twigs of ant-inhabited species from New Guinea, not typical to the west.

fused by their backs and to each other by their edges, the extreme apex of the column often sterile. The fruit is typically large and the aril deeply cut to the base of the seed. The genus can be divided into two sections. In the first, the inflorescence is branched and the flowers and branch axes form all in one episode. In the second type, a central perennial axis supports the episodic blooming of individual flowers, a habit similar to that of *Knema*. *Myristica sepicana*, a species of New Guinea, represents a divergent type: it lacks a bracteole below the perianth, a feature that diagnoses *Myristica* and distinguishes it from other Myristicaceae, except *Knema*. However, the tree otherwise looks so much like a *Myristica* that its recognition as a monotypic genus (*Paramyristica sepicana*) would likely render the rest of *Myristica* paraphyletic. Molecular evidence is needed.

These are medium to big trees of the lowland rainforest with very limited occurrence in other habitats, often with a black bole, sometimes with flaky bark. Stilt roots are more common here than in other genera and especially so in the species of swamps. The leaf stalk is often two-three cm long and somewhat sinuous, the lower surface of the blade is usually green below (copper in a few species), often thin, drying black and rapidly decaying on the ground. The nerves are more looped than in *Knema* and they are most often sharply sunken above in the dry leaf, and nearly blistered in a few species. Sterile trees are difficult to identify to species. More than in other genera of Myristicaceae, so it is not easy to become familiar with the individual species of *Myristica* because the number of species is uncertain, the variation is great, and the density is low. New Guinea is the center of species numbers, and the total is still being explored. The genus becomes less numerous and a less conspicuous representative of the family to the west, where it is ecologically replaced on dry ground by the more numerous species of *Knema*, although *Myristica* it is still abundant in swampy ground.

More than a few species are cultivated, even at relatively higher latitudes, but the nutmeg, *Myristica fragrans*, is the most famous. The economic and historical importance of the nutmeg cannot be overstated. As a reputed aphrodisiac, a hopeful cure for plague, and with a value greater than gold, it was nutmeg more than any other spice that launched the European exploration of Asia as a means of circumventing the Arab trade monopoly. Giles Milton¹ provides a popular recounting of the wars among Portuguese, Dutch and English interests that focused on little Run-Run Island, Indonesia.

The outer husk of nutmegs are commonly pickled or candied in the Sundaic Region, sold as *buah pala*. The aril is sold as the spice mace; the seed is sold as nutmeg, whole, ground or distilled to a commercial oil. Curiously, nutmeg rarely enters into the flavoring of dishes in the Malay Archipelago. It is increasingly common westward, in India and the Middle East, and reaches its greatest fame in Europe and America where breads,

cakes, pies, cider and eggnog celebrate the fragrance of a Dicken's Christmas.

KNEMA. [Greek for spike in reference to the points of the fused anthers.] 85 species, widespread as a genus, centered in the Malay Peninsula and west Borneo with many species that are both frequent and abundant. A different set of species, fewer in number, are frequent and abundant in the seasonal tropics of mainland Asia as well as north throughout the Philippines. That the species *Knema furfuraceae* and *K. conferta*, which are characteristic of the lowland Malyan forest, are also attributed as far north as southern China at 500 m is surprising, perhaps wrong.

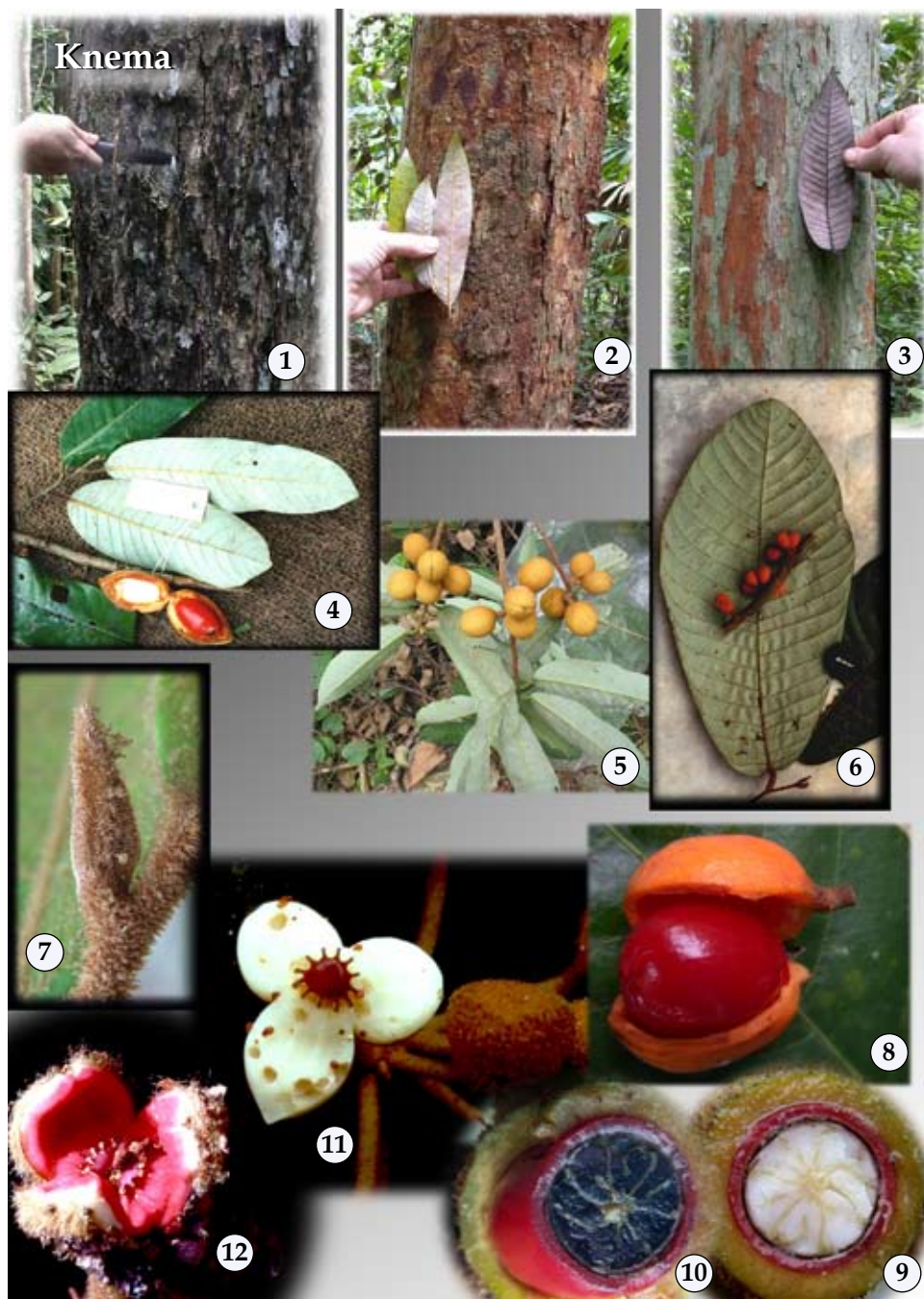
These nutmegs are especially abundant as small to medium trees. The bark is variable brown, black or mottled. The leaves are the most sturdy in the family, usually bright green above and whitish below, with a strong raised midrib. The main nerves spread from the midrib in a regular fish-bone pattern and fade near the margin, not looping. Only in the abundant *K. laurina* are the nerves sunken above. The fruits are characteristically hairy or rough red-brown granular. The genus shares with *Myristica* a median bracteole below the flower.

I might also mention the tendency to form sports or mutant varieties with odd shaped leaves. I believe it is restricted to this genus. Populations of *Knema glomerata* in the Philippines often bear a wavy invaginated margin. Another example was seen in Lambir Hills, Sarawak, in which a small patch of *Knema ashtonii* was found with every leaf split lengthwise as in rabbit ears.



Knema glomerata at Mt. Makiling, Luzon, Philippines; this population bears oddly invaginate leaves; such non-entire margins are rare among Myristicaceae, perhaps restricted to a few species of *Knema*.

¹Milton, G. 2000. *Nathaniel's Nutmeg*. Penguin Paperbacks.



Knema. 1-3, variation in mature bark; 1, *K. hookeriana*; 2, *K. glauca*; 3, *K. conferta*; 4-8, leaf blade of *Knema* is glaucous below, the nerves in a fish bone arrangement, the fruit globose, orange with crusty red granules; 4, *K. latifolia*, Lambir, Sarawak; 5 & 8, *K. glomerata*, southern Vietnam; 6, *K. pulchra*, Lambir, Sarawak; 7, the twig apex of *K. laurina*, red hairy and typical of the family; 9-10, *K. laurina*, XS fruit 15 mm wide, natural and iodine stained, showing starch (of the genus) and ruminant endosperm (of the family); 11, *K. intermedia*, Pasoh, Malaya, red granular triangular buds, flower 7 mm wide, petals white within, spreading, staminal column is red; 12, *K. hookeriana*, Pasoh, Malaya, flower 12 mm wide, red within and weakly opening.

MAGNOLIIDS: MAGNOLIALES

MAGNOLIACEAE

NAME: From the genus *Magnolia*, as below. The name magnolia is sufficiently old and well-known as to be an accepted noun in English. The most common Malay name is *medang limo*, and in the Philippines, *patangis*. The cultivated *Magnolia chempaka* is widely known as *chempaka*.

OVERVIEW: Magnoliaceae are a small and homogenous family that are best treated as comprising two genera. The first is *Liriodendron*, the tulip-tree, a small genus of E Asia and E North American that is not further considered here, although *L. chinense* does in fact reach northernmost Vietnam. The second genus is the vast *Magnolia*, as below.

MAGNOLIA. [Commemorates Pierre Magnol, French botanist, director of the Botanical Gardens in Montpellier, d. 1715.] *Magnolia* is represented by 220 species, homogeneous with regard to the basic vegetative and floral organization, but of great heterogeneity with regard to the details of the fruit and the position of the flowers relative to vegetative growth. In the past, *Magnolia* was treated as suite of genera within the subfamily Magnolioideae; most of the small genera were small in size and controversial in delimitation. Molecular studies that included 99 species found strong support for monophyly and low molecular divergence within the subfamily^{1,2}. The majority of traditional segregate genera, subgenera and sections were discordant with the hypothetical molecular phylogeny. Although several strong constituent clades were found (for example, the sampled species of *Manglietia* - excluding the sometimes further segregated *Manglietastrum* - formed a strong clade, as did the two odd dioecious species that are sometimes placed in *Kmeria*) the small clades fell within the unresolved bulk of the samples. In particular, the well-known group of magnolias that form subgenus *Yulania* are more closely related to *Michelia* than they are to other magnolias. The natural conclusion is that the subfamily itself of 220 species should be treated as a single genus, a conclusion followed here. (Note that while there are more than a few species that lack a published name under *Magnolia*, almost of our species in tropical Asia, that is, the former *Michelia*, *Talauma* and *Aromodendron*, have valid names under *Magnolia*.)

A good introduction to *Magnolia* and its extensive literature can be found in the website of the Magnolia Society³. The greatest diversity of form is found in subtropical China and the greatest ecological importance is in E North America and E Asia. In tropical Asia, we



Magnolia philippinensis, Mt. Silanganan, Philippines (© Ulysses Ferreras.)

find about perhaps 30 species, in the lowlands and in the mountains, and in both everwet and dry seasonal forests. These include about 25 species of Mainland SE Asia (19 in Laos); about six to 10 species in Malaya (many forms now lumped under *M. liliifera* - see photographs at the Flora of Peninsular Malaysia web site); 15 or so in Borneo; seven in the Philippines, and a half dozen species scattered through the east to New Guinea but not beyond. It would be unfair to say that the magnolias of tropical Asia are in a state of chaos, although a student might be justified in thinking so, because compilation of national checklists would yield a half dozen generic names, and a great many species, subspecies, forms and

FIELD RECOGNITION: MAGNOLIA

No exudate.

The blade is typically elliptic in shape with a sharp apex, sometimes stiff.

Encircling conical stipule more or less joined to the leaf stalk, the leaf stalk grooved above, with a triangular scar at the base.

Fine venation is boxed and distinctive.

Old fertile parts often found about the tree.

FIELD CONFUSION

Gironniera (Ulmaceae) the leaves alternate not spiral clustered, and the ultimate stipule set at an angle.

Some Moraceae bear a pointed encircling stipule, but with copious white exudate.

Barringtonia leaf is often of similar outline, but the blade typically has a few teeth in the upper margin.

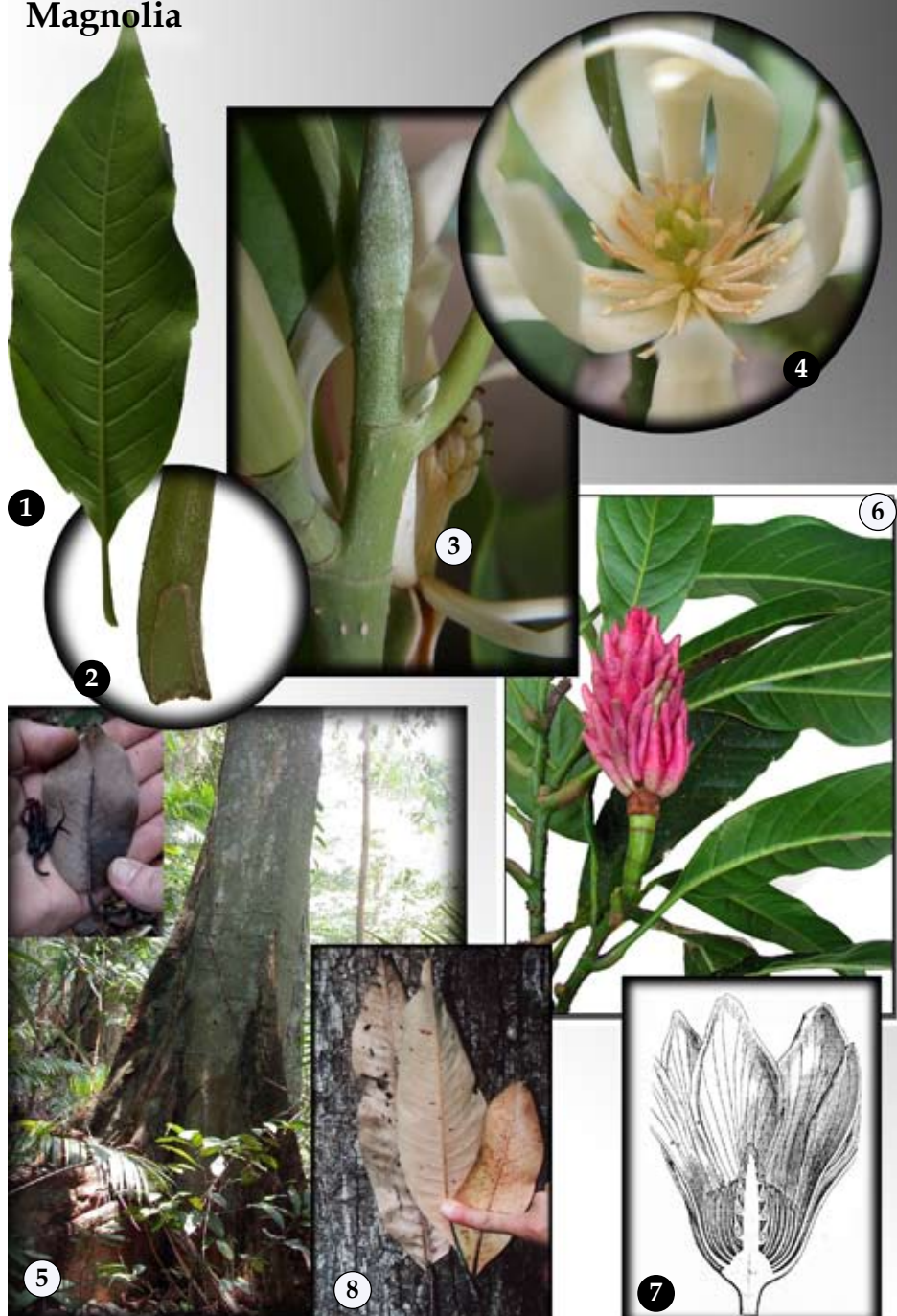
Iringia is similar in the pointed stipule encircling the twig; the leaf stalk lacks a triangular scar, but can be confused with *Magnolia* [*Aromodendron*] *elegans*.

¹Kim, S, *et al.* 2001. American Journal of Botany. 88: 717-728.

²Azuma, H, *et al.* 2001. American Journal of Botany. 88: 2275-2285.

³The Magnolia Society. (<http://www.magnoliasociety.org>).

Magnolia



Magnolia. 1-4, cultivated *chempaka*, *Magnolia* [*Michelia*] *x alba*. 1, leaf with elliptic blade and distinct stalk; 2, the base of the stalk is fused to the conical stipule and leaves a triangular scar; 3, the apical bud of the twig is strong, stout, and sharp-pointed; 4, the flower shows the numerous parts in spiral arrangement characteristic of the family; 5, *Magnolia* [*Aromadendron*] *elegans*, 45 cm DBH, with short stout buttresses, small elliptic leaves (lacking a scar on the stalk) and fallen flowers; 6, *Magnolia* [*Talauma*] *candolei*, young fruit with many free independent carpels, here, brightly colored; 7, TS of the flower; 8, leaf and bark of *Magnolia baillonii*, Huai Kha Khaeng, Thailand. (Illustration adapted from BAILLON *loc. cit.*; photograph 6, © Leonardo L. Co.)

varieties all switching back and forth in synonymy. These much-neglected trees simply suffer from the fate of so many of our trees: exhaustive analysis of scanty collections. The priorities should be further field study coupled with an aggressive campaign to cultivate all of our native species, and the efforts cannot begin too soon.

Some of our species of *Magnolia* are large trees that may reach 80 cm DBH and 30 m in height, but most species are of small to medium stature and a few are multi-branched shrubs. The main axis bears spirally arranged leaves; the lateral branches bear leaves that at maturity are arranged either alternately in a plane or clustered in rosettes. The position of flowers relative to vegetative growth varies among species. Flowers either terminate a leafy branch or terminate a short leafless branch that lies axillary to the foliage leaves of the main branch. Further variation is found in whether the vegetative branches grow episodically with new growth in arrested buds, or grow continuously. Finally, species can be deciduous or evergreen.

The bark of *Magnolia* is bitter and aromatic; the plant body bears alkaloids and oil-cells in the parenchyma. The wood is homogeneous within the family and of a very simple type. The vessels are small and evenly distributed. Solid plugs of silica-dioxide are common, with some samples showing an estimated 8% volume of silica, the highest silica content known among vascular plants. The leaf blade is simple and leathery. A stipule encircles the twig, enclosing the terminal bud and often joined to the inner face of the leaf stalk in such a way that when it falls away it leaves a distinctive triangular scar on the base of the stalk.

Magnolia flowers are typically large, 5-10 cm across, solitary and bisexual except in those species formerly distinguished as *Kmeria* where they are unisexual dioecious. The floral axis is elongated, the floral parts arranged

spirally from the base, beginning with petal-like organs that number six to 20 and may vary slightly or greatly in form. Petals are followed by numerous (50-200) stamens, exclusively fertile, spirally arranged, maturing centripetally, with the anthers linear, two-locular, dehiscent introrsely or latrorsely (compared with extrorsely in *Liriodendron*). The stamens are followed by a long or short intervening space, then a series of up to 200 essentially free carpels; each carpel bears two (-20) ovules. The gynoecium is either sessile or stipitate, the carpels can be free or fused. The mature fruit is highly variable. It can consist of free carpels that split open along the dorsal and/or ventral suture, or the carpels can be variously fused and break apart in different ways. Rarely the fruit is indehiscent.

Magnolia species are found in almost every lowland forest, but typically with no more than one adult tree per 10 ha. In dry seasonal forests and in mid-elevation mountains, *Magnolia* can be more abundant. The flowers are strongly fragrant, but do not produce nectar, at least this is true of those few species that have been studied. Flowers of North American species are protogynous; beetles enter the flowers early, are covered in pollen which they transfer to the next flower they visit. The stigma is receptive only prior to the maturity of the anthers thus assuring cross pollination. Pollination in species of tropical Asia has not been studied. The flowers of some, perhaps all, species heat during the night, which if nothing else greatly aids the dispersal of the fragrance. Coleoptera are likely the main pollinators, but other insects visit the flowers.

Two species are commonly cultivated in our region. *Magnolia* [*Michelia*] *champaca* is a small tree with yellow flowers native to India, known as *chempaka*. *Magnolia* x *alba*, of hybrid origin, is a larger tree with bright white bark and white flower.



MAGNOLIIDS: MAGNOLIALES

HIMANTANDRACEAE

NAME: Because names compete within ranks, the family name is Himantandraceae, based on the old genus name *Himantandra* - from Greek for a leather strap in reference to the anther - even though the sole genus is *Galbulimima*.

OVERVIEW: Essentially a single species, as below.

GALBULIMIMA. [Latin, galbulus-mimus, fruit resembles a fleshy cone.] Usually treated as a monotypic genus represented by *Galbulimima belgraveana*, with commonly published synonyms under *Eupomatia* and *Himantandra*, but also as two, three or perhaps more undescribed species differing in stature and size of parts. These are especially common in New Guinea but also in the Solomon Islands and northeast and south Queensland, Australia, and west at least to Sulawesi. It should be looked for in the Mindanao and eastern

Galbulimima



Galbulimima belgraveana, drawn from specimens including the type, *Forbes* 799 from New Guinea; flower about 1.5 cm across with spirally arranged tepals; the fruit about 3 cm across.

Borneo. *Galbulimima belgraveana* is a common tree in New Guinea in *Nothofagus* forests at 1200 to 2700 m elevation. A buttressed tree to 35 m tall and 60 cm DBH, with a bitter taste and resinous smell, with leaves as in Annonaceae or Illiciaceae. Copper-colored peltate scales of varying density cover the twigs, the underside of leaves, petioles and flower stalks. The flowers are solitary and axillary, bisexual and odd in the more or less

two-part and overlapping calyx-like bracts, and the indefinitely numbered creamy petal-like perianth. The flower is said to emit a strong unpleasant odor. The fruit is fleshy and indehiscent to three cm diameter. Each carpel bears a single small flat seed. The plant body is full of alkaloids that have attracted much attention because, among other effects, they are highly psychoactive.



MAGNOLIIDS: MAGNOLIALES

ANNONACEAE

NAME: From the genus of Neotropical trees *Annona*, the name derived from a local name in Brazil. In reference to the common cultivated fruit, we might call this the *sour-sop* family or, by use of a Malay name, the *mempisang* family.

OVERVIEW: A well-defined monophyletic family of 130 genera and 2500 species, pantropical and exclusively woody and tropical except for the nearly herbaceous *Asimina* found northward to the American Great Lakes. Most genera are confined exclusively to one or another continent except for *Xylopia* (world-wide) and *Anaxagorea* (Asia and America) and a few Asian genera, such as *Popowia*, with putative African species. Within our focal area, the family is represented by roughly 860 species of trees in about 32 genera, with a center of richness and abundance in the lowland equatorial forests but with good representation everywhere except for most dry-seasonal lands and mountains above 1000 m.

The family is in the midst of a complete review in the light of new molecular data^{1,2,3}. While the results are far from complete and the consequences are yet to be implemented, significant changes are anticipate especially within the largest genus, *Polyalthia*. At present, the phylogeny is little more than an outline, and yet it is full of interesting insights. The main conclusions are as follows:

1. The most significant conclusion is in the negative, but usefully so, in that the molecular phylogeny is discordant with past morphologically based tribal arrangements. While the resolution of DNA-based groups is poor and no new system can be introduced, no old systems can be supported. In particular, the key features in past tribal alliance, such as valvate versus imbricate corolla and the miliusoid stamen connective, do not cluster with molecular clades.

2. The conclusion, "Most genera are monophyletic" is true, but we should bear in mind that about half the genera include only a few species, so with sparse sampling a

conclusion of monophyly is not too surprising. The key question lies in the relationship of the small genera to the species-rich genera such as *Goniothalamus*, *Xylopia* and *Polyalthia* of which only the last had a sampling adequate for testing and it proved widely polyphyletic.

3. The genus *Anaxagorea* is sister to the rest of Annonaceae and adjacent to a basal, but likely non-monophyletic group that includes the Asian trees of *Cananga*, *Cyathocalyx* and *Mezzettia*, two other African genera and one American.

4. Derived from within this basal group is a strongly supported clade comprising two sister clades. The first is termed the "long-branch clade" in reference to the wide molecular separation from the other taxa; it includes many Neotropical taxa related to *Annona*, most of the Asian genera of lianas plus the genus of Asian trees, *Goniothalamus*. The second grouping is called the "short-branch clade" and is especially genus-rich and

FIELD RECOGNITION: ANNONACEAE

Twig and trunk without exudate.

The leaves simple, without stipules, a relatively short stout stalk.

The midrib is flat to shallow sunken on the upper surface (except for *Stelechocarpus*, many lianas and many exceptions in the Neotropics).

The bark of the twigs peel easily to reveal a fishnet pattern of fibers overlaying the wide rays.

Looking up into the canopy the branches often long, typically numerous and of a similar size, arrayed spirally from the mast-like trunk.

On smaller trees one can usually see that the branches are borne at a clearly divergent angle from the leaf axil.

The blade without glands but with varied odors of ethereal oils.

Often enough in flower or fruit, these distinctive and quickly identifiable to family.

FIELD CONFUSION

Magnolia differ most obviously in bearing a conical stipule that form ring scars at the node

Myristicaceae, the twig peels weakly and if at all then lacks the reticulate pattern beneath the bark; also these bear a red hairy apex and red exudate.

Diospyros, the twig is non-peeling, the leaves along the twig are of varying sizes and the blade usually includes yellow or black laminar glands.

Some Lauraceae are similar, the twig is non-peeling, the leaf stalk tapers from twig to leaf.

¹Bygrave P. 2000. Molecular systematics of Annonaceae. Ph.D. dissertation, University of Reading, Reading, UK.

²Mols, J., et al. 2004. American Journal of Botany. 91: 590-600.

³Richardson, J., et al. 2004. Philosophical Transactions of the Royal Society of London. B. 359: 1495-1508.

Phylogeny of Annonaceae

The phylogeny below is an adaptation of the two molecular studies cited in the introduction to the family, restricted to the genera of trees in tropical Asia. Note that most of the relationships among genera remain unresolved, that some genera were not included in the molecular studies, and that *Polyalthia* is found to be polyphyletic.

	GENUS	TREES OF TROPICAL ASIA
	<i>Anaxagorea</i>	5-9, small trees of patchy distribution and local abundance, blade with loose reticulate nerves, ballistic dispersal .
	<div>BASAL GRADE</div> <div>?</div> <div><i>Cananga</i></div>	2, each distinctive, in dry seasonal places.
	<div><i>Cyathocalyx</i></div>	36, widespread tropical Asia, of two types, petals pinched near base, large fruit, few carpels.
	<div>?</div> <div><i>Monocarpia</i></div>	5, Sundaic Region, as in <i>Cyathocalyx</i> s.s., leaves dry shiny brown, looped nerves.
	<i>Mezzettia</i>	4, Sundaic Region, large tree, consistent but very low density, with thin papery leaves.
	<div>LONG-BRANCH CLADE</div> <div>INCL. ASIAN LIANAS</div> <div><i>Dasymaschalon</i></div>	20, shrubs, dry seasonal Asia.
	<i>Desmos</i>	25, mostly lianas, ill-formed shrub, leaf white below, string-of-pearl carpels.
	<i>Disepalum</i>	9, shrub, often of full sun, habitat, sepals .
	<i>Goniiothalamus</i>	100, all stems with 2-ranked leaves.
	<i>Xylopia</i>	160, pantropical, about 26 in Asia, many leaves with obscure even nervation, wet ground with stilt roots, three sided floral bud, transverse septate anthers .
	<div>SHORT-BRANCH CLADE</div> <div><i>Polyalthia</i></div>	100, tropical Asia, polyphyletic, six petals, numerous carpels, typically one seed with circumferential groove, anthers shielded by connective.
	<i>Maasia</i>	6, medium trees of Sundaic Region, glaucous white lower leaf surface, some with white bark.
	<i>Enicosanthurum</i>	20, tropical Asia, some locally common, congeneric with some <i>Polyalthia</i> , traditionally differs by overlapping sepals and thick petals, stamen connective truncate.
	<i>Dendrokingstonia</i>	1, Malaya, mature carpel with several seeds in 2 rows.
	<i>Trivalvaria</i>	5, S Thailand to Borneo, scalariform nervation, carpels elongate, sessile extra-axillary flowers, blunt style.
	<i>Miliusa</i>	40, India to Australia, shrubs and small trees, low density, saccate petals, anthers not shielded by connective.
	<i>Orophea</i>	41, India, tropical Asia, mostly rare shrubs, mitre-form flowers.
	<i>Alphonsea</i>	25-40, especially Mainland SE Asia and Sundaic Region, small to large trees, most rare.
	<i>Platymitra</i>	2, common large trees, dry seasonal parts of tropical Asia.
	<i>Phaeanthus</i>	12, India to New Guinea, common small trees, leaf dries black, papery, scalariform nerves.
	<i>Marsypopetalum</i>	1-2, Sundaic Region and Java, dry leaves bright green, purple twig.
	<i>Meiogyne</i>	24,,like <i>Polyalthia</i> but 1-4 seeds per carpel, blunt stigma.
	<i>Sageraea</i>	9, India to tropical Asia, leaf stiff, varnished.
	<i>Stelechocarpus</i>	5-6, tropical Asia, midrib strongly raised above.
	<i>Mitrephora</i>	48, India, China to Australia, mitriform flower, outer petals larger than inner.
	<i>Pseuduvaria</i>	52, Mainland SE Asia to Australia, mitre-form flower, outer petals equal to or smaller than than inner.
	<i>Neouvaria</i>	4, Sundaic and Philippines.
	<i>Popowia</i>	30, India to Australia, especially Sundaic Region, (also Africa), abundant small trees, leaf dries finely pimpled, some with stellate hairs, small flowers.

species-rich. It includes *Polyalthia*, which proves clearly polyphyletic with species scattered in perhaps six groupings. It also includes a distinct clade, rich in genera and species, that is restricted to South America.

5. Some clades within the family are morphologically cryptic.

The Annonaceae are so uniform in vegetative form that if a student carefully studies one example they can confidently and consistently recognize the family. But that it is not true of the genera in Asia because most overlap one another in details of leaf form.

Among trees, we find two patterns of growth and vegetative organization. The most common pattern consists of a tree of two branch type: an monopodial upright stem in which the leaves are arranged in a spiral, and lateral branches in which the leaves are strictly two-ranked in a plane. In this type the lateral branches are typically long and drooping, the twigs in a zig-zag pattern, each leaf with one or more axillary buds from which other branches grow all within the same plane. The organization and growth of the upright stem is more complex. Each of the spirally arranged leaves bears in the axil a complex cluster of buds; the most eccentric of the buds forms a lateral shoot that at maturity diverges at an angle to that plane formed by the leaf midrib and the upright shoot. The interpretation of the system is complicated by the rapid growth of the lateral shoot which expands so quickly that it becomes larger and more conspicuous than the apical shoot itself.

The second pattern of growth is seen among the liana genera and, among our trees, in *Goniothalamus*, and also in the cultivated *Annona*. In these, all stems, both upright and lateral, are organized as in the lateral branch of the first type, that is, with leaves in a strict two-ranked arrangement. These plants give the impression that they are composed entirely of lateral branches, and this is especially strong in those diminutive trees of *Goniothalamus*, such as *G. velutinus*, which consist of only a single arched frond-like axis.

The abundance of lianas among Annonaceae in tropical Asia is in sharp contrast with the family representation in tropical America where the liana habit, while not unknown, is decidedly rare. The difference could be phyletic as might be hinted at in the clustering of Asian liana genera in the basal grade - and note the absence of lianas among the related families of Magnoliaceae and Myristicaceae.

The twig construction is distinctive and characteristic of the family. Twigs bear septate pith and rays that are wide and regular - the bark peels easily from the twig to reveal a fishnet pattern of fibers, while a slash of the trunk reveals a colored network beneath. Other vegetative features are noted under field recognition.

The flowers are axillary or in tightly condensed clusters, only rarely in large inflorescences, and these are restricted to the genera of lianas. Flowers are typically less than two cm across, fragrant, with brittle thick fleshy parts, most often bisexual (but unisexual-dioecious in some *Pseuduvaria* and a few others). The floral axis is reduced, often broad, squat, the perianth parts imbricate or valvate, spiral or cyclic, typically in threes, the perianth parts often all similar, then typically nine in three whorls of three, but sometimes differentiated as three calyx lobes and six petals, the petals equal, sub-equal or very different in size and shape and color. Stamens number 25 to 100, maturing centripetally, spirally arranged, rarely three or six-whorled, free of the perianth, all equal and free of one another; exclusively of fertile stamens (usually), or including staminodes (some lianas in *Uvaria*); the anthers extrorse and open by longitudinal-slits. The carpels number 10 to 100, or reduced to a few, always free among Asian taxa, often with one to several basal ovules. Each carpel develops as a stalked berry usually called a monocarp. In most Asian Annonaceae, the fruit looks like a bunch of bananas - thus the Malay name *mempisang*. Seeds are large, few, endospermic and, in contrast with Magnoliaceae, ruminant.

Most Annonaceae are thought to be pollinated by beetles, a conjecture based on a hopeful extrapolation to thousands of species from very few observations. The few studies of pollination among Asian Annonaceae deserves special notice. Weevils have been found as pollinators in *Xylopia*⁴ and *Polyalthia*⁵ the former with floral heating and the latter with a pollen chamber. The flowers of *Popowia pisocarpa* are exceedingly small for a member of the Annonaceae and the chamber is all but closed and obstructed by the stigmatic head blocking all potential pollinators except thrips⁶. Those Annonaceae that bear open flowers without a pollen chamber are ambiguous with regard to pollinators. The abundant lianas of the genus of *Uvaria* bear large open flowers, often bright red; one species bloomed a night with a odor of rotting wood or mushrooms and was pollinated by cockroaches⁷. The open mitriform flowers of some Annonaceae are curious; at least in *Pseuduvaria* they appear to be pollinated by flies.

Among the Annonaceae of Asia, the majority of diaspores are fleshy berries less than one cm across, swallowed whole, the seed presumably gut-passed by small mammals, primates, and understory birds. A few other dispersal syndromes are known: some *Xylopia* are dehiscent with black seeds against a bright red flesh, and *Anaxagorea* is ballistic, the shiny black seed is pushed violently from the drying carpel. Large fleshy syncarps, such as those of the cultivated *Annona*, are not found among Asian trees.

More than a few species have delayed chlorophyll development in the new leaves, and in some the early leaves are red or white.

Two genera, *Mezzettia* and *Miliusa* (= *Saccopetalum*) grow to a size that produces timber of significant volume; however, the quality has always been regarded as inferior and they have attracted little commercial inter-

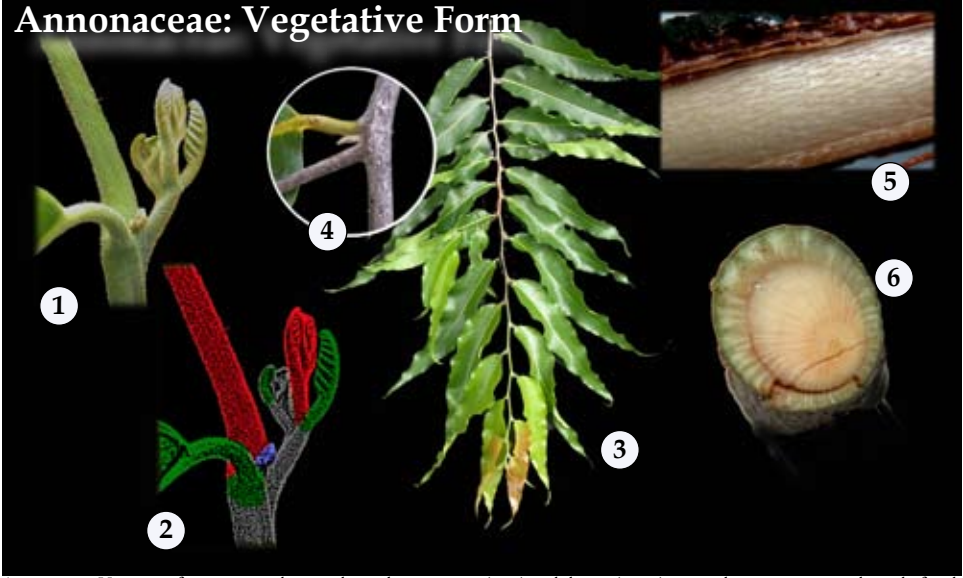
⁴Ratnayake, R, *et al.* 2007. International Journal of Plant Science. 168:1255-1268.

⁵Ratnayake, R, *et al.* 2006. International Journal of Plant Science. 167: 483-493.

⁶Momose, K, *et al.* 1998. Biotropica. 30: 444-448.

⁷Nagamitsu, T, *et al.* 1997. American Journal of Botany. 84: 208-213.

Annonaceae: Vegetative Form



Annonaceae: Vegetative form. 1 & 2, the upright, orthotropic axis (gray) with leaves (green) in spiral arrangement; in the axil of each leaf is a cluster of buds, the most eccentric of which develops as a lateral shoot (red) overtopping the growth of the apical meristem. 3 & 4, in lateral branches the leaves are two-ranked, with axillary buds singly or in clusters; 5 & 6, the thick bark of the twigs peels easily to reveal a fishnet pattern of fibers intervening among the wide rays.

est. The American genus, *Annona*, contributes many commercial fruits as described below. The flowers of the native *Cananga odorata* are the source of the fragrant ylang-ylang oil. As ornamentals, the family has been much neglected, which is surprising because the flowers are fragrant while the trees demand little care. The Indian tree, *Polyalthia longifolia* is planted everywhere in Asia specifically because it is tough, drought tolerant and insect resistant.

ANAXAGOREA. [Commemorates Anaxagoras, d. 428 BC, one of the first Athenian philosophers.] About 20 species, more than half in Central and South America, and then five to nine closely related species in lowland forest and lower wet mountains of Asia from Sri Lanka and Myanmar to Indochina, and throughout the Sunda Shelf to the Philippines.

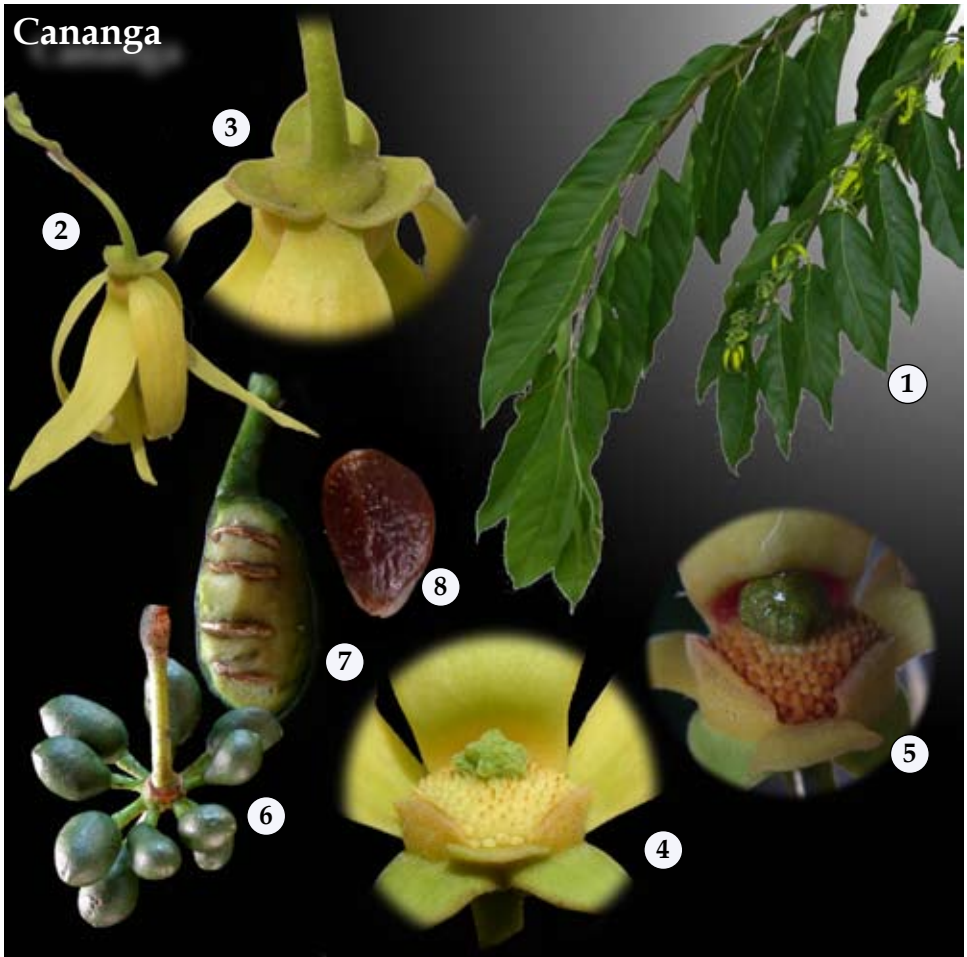
These are all small trees, not much over 2-5 cm DBH, sometimes forming an undergrowth not more than one m tall at maturity. The blade is broad and the venation is a loose open reticulation. The distribution is patchy, at local scales as well as regionally. Where they occur, *Anaxagorea* can be the most abundant of small trees, a local abundance presumably driven by the ballistic dispersal. And yet we find many seemingly appropriate forests where they are absent altogether.

The flower bears three valvate sepals and three or six valvate petals in two whorls (some variants with parts in fours), the inner slightly smaller than outer, somewhat spoon-shaped, the many stamens with extrorse anthers some sterile or not, with connectives slightly bent outwards with an extended tongue-shaped apex; the carpels

have a U-shaped opening at the stigmatic part with a groove on anterior side. The mature carpel is stalked and club-shaped; it splits as it dries and pushes out the shiny slippery black seed to a distance of 2-3 m.



Anaxagorea javanica, individual stalked carpels, dehiscent with ballistically dispersed seeds, 2 cm DBH trunk to the right; inset, *A. luzonensis*, flower.



Cananga odorata. 1, long drooping lateral branch with two-ranked leaves and numerous axillary flowers in various stages of development; 2 & 3, flower with nine perianth parts, usually described as three short triangular sepals and six equal petals; 4, numerous stamens spirally arranged about the numerous free carpels; 5, in a later stage the stamens have dehiscent, the stigmatic surface now becomes sticky; 6, the mature carpels; 7, a single carpel partially dissected to show the several flat seeds embedded in the flesh; 8, the pimpled seed with a small white aril at the base.

Anaxagorea is of special phylogenetic interest in that it appears to be basal to the rest of the family, a result a little surprising in that the dehiscent fruit and ballistic dispersal would normally be presumed to be highly derived. The disjunct occurrence of species between America and Asia is itself rare in the Annonaceae, shared only with the pantropical *Xylopia* - but, unlike the heterogeneous *Xylopia*, the species of *Anaxagorea* are astonishingly similar to one another. Such a lack of divergence is surprising in the purportedly basal genus.

The seeds smell of camphor and according to BURKILL *loc. cit.* were once used to preserve clothes.

☞ - Annonaceae Basal Grade - ☞

CANANGA. [From the Malay name.] A genus of two species, native to seasonal places in tropical Asia,

but cultivated with mixed success elsewhere. The flowers bear three valvate sepals, six valvate petals in two roughly equal whorls, connectives with lance-shaped apex, the mature carpels oblong, stalked with several flat pimpled seeds that bear a small white aril-like structure at the base. The complex history of the name *Cananga* has been recently reviewed.

Cananga odorata is a small tree of poor form, a weak main trunk and numerous long swooping branches, almost liana-like and can be trained as such. It is known widely as *ylang-ylang* or *kenanga*. The flowers are sold on the street, especially in the Philippines, and also grown commercially for two perfumery products. *Ylang-ylang* oil is now grown mostly in Madagascar and Comoros, while *kenanga* oil is mostly grown and used locally in



Cananga latifolia. Left, in lowland forests of Vietnam, note the large flexible hairy leaf with invaginated base; Right and inset, the same species in western Thailand, large tree with shaggy bark.

Java. The green-purple fruit are utterly inedible: hard, thin-fleshed and filled with sticky turpentine-smelling resins. The seeds are flat and as slippery as watermelon seeds. The phylogeny and biogeography of the species deserves better study. Although it is claimed as a native tree throughout tropical Asia, it seems to prosper in strongly seasonal climates; I would not be surprised to find that it originated in India, spread with early trade and naturalized elsewhere.

Cananga latifolia is a large tree with shaggy gray bark and large papery leaves with a broad somewhat invaginated leaf base and softly hairy lower surface. It is an important element in the dry-seasonal forests of Mainland SE Asia where it seems to prefer open deciduous habitats. It can be found as far south as Perlis and Langkawi in the Malay Peninsula and would not be surprising in the dry-seasonal parts of Sumatra and Java.

CYATHOCALYX. [Greek, the type species from Sri Lanka has a fused cup-shaped calyx, otherwise unique in the genus.] 36 species, broadly distributed in Asia from India to New Guinea. At least the fast-growing gap species are known in Malaya as *antoi*, in Borneo as *selamo*.

The genus includes two kinds of trees, formerly treated as genera or sections, differing in form and ecology. Most species are of the *Drepananthus*-type, these are fast-growing trees of gaps and roadsides with a clear mast pole that bears thick plagiotropic branches, the branches more or less deciduous as a whole; the leaves stiffly stellate hairy with a midrib sunken above. The flower bears



Cyathocalyx. 1-3, *Drepananthus* type; 1, *C. pruniferus*, Pasoh, Malaya, a fast growing tree in a forest gap with upright stem and numerous lateral branches at right angle to the trunk; 2, large blade with pruniferous lower surface; 3, the type material of *C. angustipetalus*, Lambir, Sarawak, a flowering branch, the flowers with constriction in the lower petal; 4-6, *Cyathocalyx*-type, *C. martabanicus*, Thailand, shade-loving trees with glabrous leaves, 4, flowering branch with constricted petals; 5, smooth bole with bright white inner bark; 6, large fruit with several seeds.

numerous carpels, the individual berries are small. In at least *C. pruniferus*, perhaps other species, the three inner petals are oddly thick and densely glandular emitting a nocturnal fragrance as powerful and as magical as that of *Cananga*.

The *Cyathocalyx*-type are forest trees of dry seasonal and equatorial lands. They include *C. martabanicus* of Thailand, commonly abundant in semi-evergreen forests but fire-sensitive, and *C. globosus* in the Philippines and only *C. sumatranus* in the Malay Peninsula. All bear glabrous leaves or with thin simple indumentum, the midrib on the upper leaf surface is flush with the surface. Here the flower bears a single carpel that develops as a large fruit. As in many Annonaceae, one finds all stages of floral and fruit development present simultaneously, the flowers change in color from green to yellow before withering. The seeds of *C. globosus* in the northern Philippines are reputedly chewed as a substitute for *Areca*.

MONOCARPIA. [Greek, one-fruit, in reference to the single mature carpel, which is deceptive, because some species bear two mature carpels.] Often wrongly described as monotypic, *Monocarpia* includes perhaps five species distributed from southern Thailand, to Malaya, Sumatra and Borneo. The different species appear to have different restricted ranges, each relatively abundant where they occur.

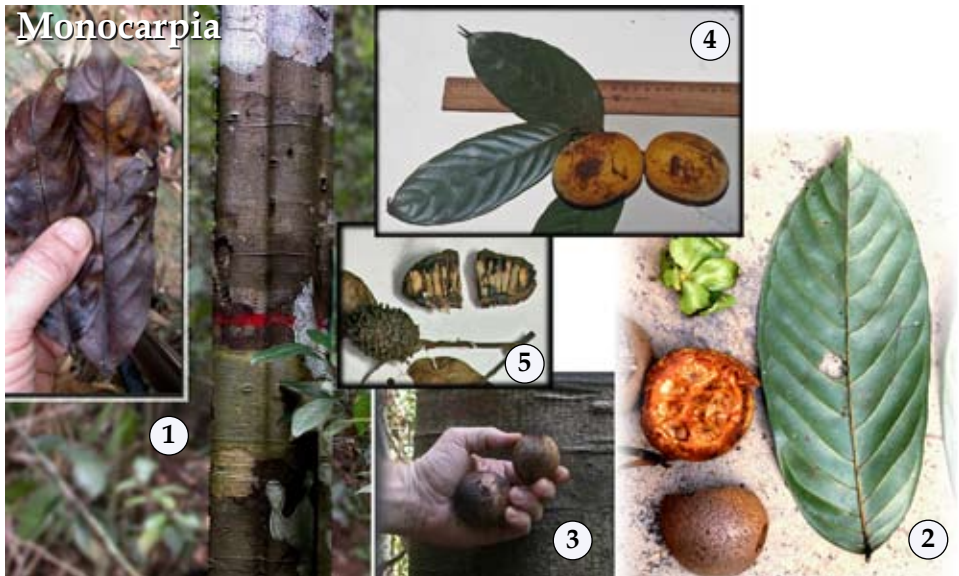
Some of the molecular evidence cited above (for *trnL-trnF*, but not *rcbL*) would place these trees toward the base of the short-branch clade. However, neither type of *Cyathocalyx* was sampled, and so for now I keep *Monocarpia* next to *Cyathocalyx*.

These are medium trees of the lower canopy. The leaves appear to be an exaggeration of the *Cyathocalyx*-

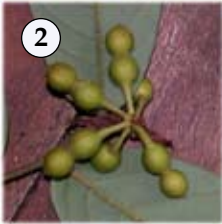
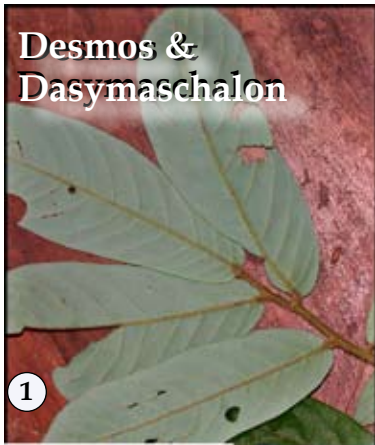


Mezzettia. 1, *M. macrocarpa*, Lambir, Sarawak, 18 cm DBH; 2, dry leaf from mature tree, thin papery dark glossy brown-purple; 3, leaf of juvenile, scaled to tree diameter; 4, a large example of *M. parviflora*, sourced in Borneo, cultivated at Bogor Botanic Garden, Indonesia.

type and can be recognized to genus by the prominent regular nerves that loop within the margin; the midrib is sunken above and bears sparse simple hairs, and dries glabrous shiny brown to black. The flowers are roughly as in *Cyathocalyx* but the petals not arched over the



Monocarpia. 1-3, *M. marginalis* of Peninsular Malaysia; 1, shiny brown leaf with looped nerves, typical cankerous bole; 2, fresh leaf, fruit with globe-like single carpels, gray-brown when ripe, numerous seeds; 3, fruit and trunk; 4, *M. euneuna* of Borneo with similar leaf but paired carpels, orange when ripe; 5, the peculiar walnut-like carpels of *M. borneensis*, Lambir, Sarawak.



1-2, *Desmos* cf. *chinensis*, Vietnam lowlands, glaucous slightly hairy lower leaf surface, the leaf base invaginated, the fruit like a string of pearls; 3, fruit of *Dasymaschalon clusiflorum* from the Philippines; 4, drawing of *Dasymaschalon blumei*, adapted from *Icones Boreales*, Vol. I, Plate 73, published in 1897. (Photograph 3, © Leonardo L. Co).

sexual organs nor with the inner three falling away in one piece; the carpels one to few, seeds one, a few or up to 10 in two rows. The ripe carpels are either large and globose, or in the remarkable species of Borneo, *M. borneensis*, with a deeply wrinkled and folded outer wall. *Monocarpia marginalis* is an abundant tree of Malaya, the type from Bangka. *Monocarpia euneura* is a similar tree from Borneo, the fruit differs from the Malayan tree in the elliptic shape and orange color.

MEZZETTIA. [Commemorates I. Mezzetti, the teacher of the great Oduardo Beccari.] Four species, Malaya, Sumatra, Borneo, to Maluku. It seems only in Borneo is a local name applied, *kepayang babi*, for the resemblance of the fruit to *Pangium*, but that name is applied to other unrelated trees as well. These are among the biggest Annonaceae, and the family's only very large tree in the lowland equatorial forest. The plots at Pasoh and Lambir recorded a single species each. The maximum diameter was 70 cm; growth rates were about 0.5 cm per year in trees of the 10 cm DBH class, but almost negligible in larger trees. The leaves are thin, coriaceous, similar to *Alphonsea*, flat and with broad open reticulate venation, the midrib broad and flat above, flush with upper surface and prominent beneath. The leaf together with the large size of the mature tree help make the genus recognizable.

The flower is small, in axillary clusters, with three small valvate sepals, six small valvate petals, green,

spreading, flat, linear, the inner smaller than the outer; stamens nine to 12 with introrse anthers, the connectives truncate and covering the anther cells from above; distinctively a single carpel, flask-shaped, tapering into the flat-topped horseshoe-shaped stigma; two ovules. The mature carpel is elliptic or globose with hard walls, bearing two large seeds. These trees are fairly consistent in the lowland forests, never surprising, but they never seem to be abundant. Nonetheless, as large trees, they can produce fruit and seeds in local abundance. Peter Lucas and colleagues studied the details of the large seed, which has a structure unique among Annonaceae that prevents mammalian predation while it allows effective germination⁸.

☞ - Annonaceae Long-Branch Clade - ☞

DASYMASCHALON. [Greek, reference to the hairs in the nerve axils of the type species.] About 20 species of the seasonal parts of tropical Asia, especially Indochina, Thailand and Philippines, and seasonal Indonesian Islands, not common in the Sundaic Region. These are chiefly multi-stemmed shrubs and a few small trees of pole size reaching the lower canopy. The Thai species were recently revised⁹. The flowers are sometimes remarkably large and attractive, distinguished by three sepals and three petals all valvate, the petals cohering

⁸Lucas, P., et al. 1991. Functional Ecology. 5: 545-553.

⁹Wang, J., et al. 2009. Systematic Botany. 34: 252-265.

about the reproductive organs all along their edges, appearing to be entirely closed. Presumably, at least the petal bases open at night to allow the entry of pollinators. The fruit are usually long and of the string-of-pearl form, with a constriction between each of the several seeds.

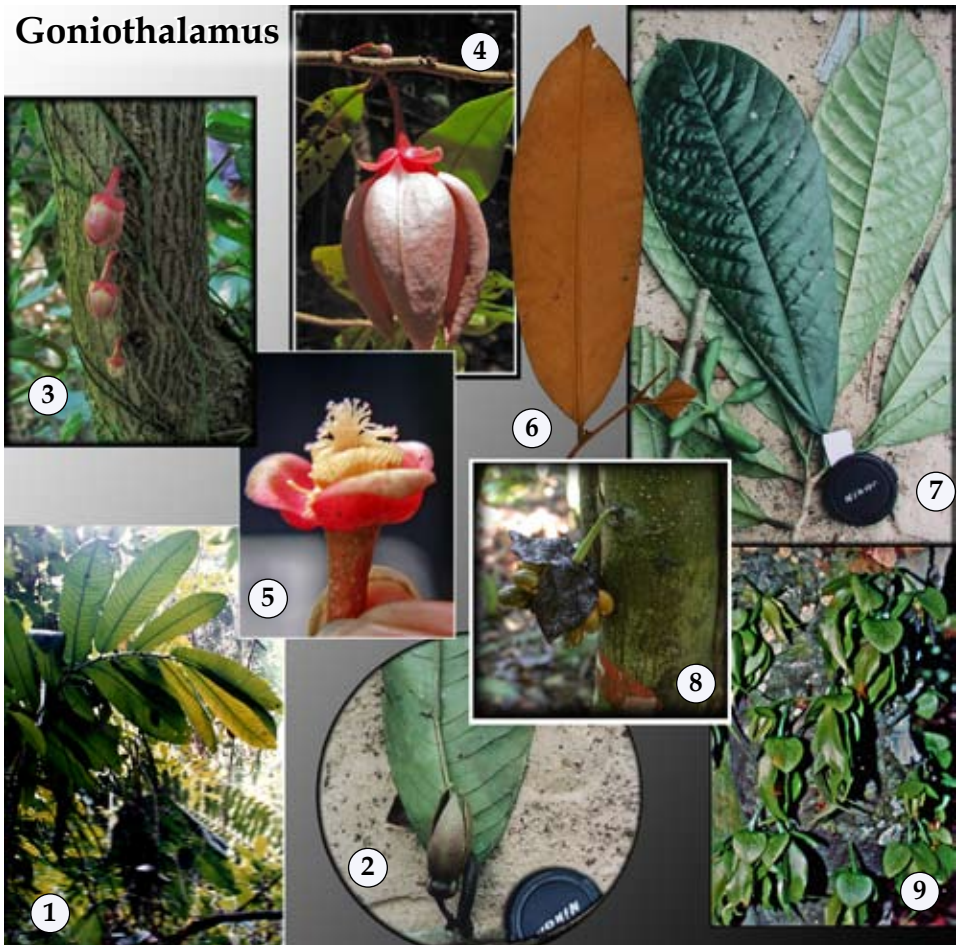
DESMOS. [Greek, bond, chain, perhaps in reference to the string-of-pearl fruit.] A genus of about 20-25 species, several are widespread and abundant, especially *Desmos chinensis*. These are woody lianas for the most part, sometimes accepting a free-standing habit, but seeming to revert to the liana form when required. Many species bear a glaucous lower leaf surface and a leaf base that is a bit invaginated. The fruits are of the string-of-pearl form, identical to that of *Dasymaschalon*. The flowers are

large and petaloid as in *Dasymaschalon*, but differ from that genus in that there are six petals rather than three, and the petals are joined only at the base while free and spreading for most of the length.

DISEPALUM. [Greek, two sepals.] nine species, Mainland SE Asia to Borneo, including *Enicosanthellum* following the recent revision of the genus¹⁰. As the name suggests, some of the species are odd in having only two sepals; others, such as *Disepalum coronatum*, are even more strange in that the petals are fused into a red petaloid cup. A further oddity of the genus is that the stalk of the monocarpis is evidently derived from the floral receptacle rather than the carpel as in all other Annonaceae.

¹⁰Johnson, D. Brittonia. 41: 356-378.

Goniothalamus



Goniothalamus. 1-2, *G. uvarioides*, Sarawak; 1, mature tree with a single arching frond, two-ranked leaves; 2, the flower with 3 small spreading outer parts and 3 large thick inner petals; 3-5, a common but still unidentified *Goniothalamus*, Philippines, note the flowers are in a single line reflecting the 2-ranked leaf arrangement; 6, some species bear leaves that dry with obscure nervation, often red, *G. woodii*, Sarawak; 7, large fleshy leaves of *G. longistipitatus*, Sarawak, with monocarpis elongate; 8-9, *G. tortipetalus*, Malaya, example of a larger tree type, cauliflorous, thick green petals dry and fall as carpels mature. (Photograph 3, © Leonardo L. Co, 4, © Ulysses Ferreras.)



Goniothalamus velutinus, Lambir Sarawak, typically grows as a single arched stem with leaves in distichous array, sometimes blooms at no more than 1 m in height, with flowers on the stem below the leaves.

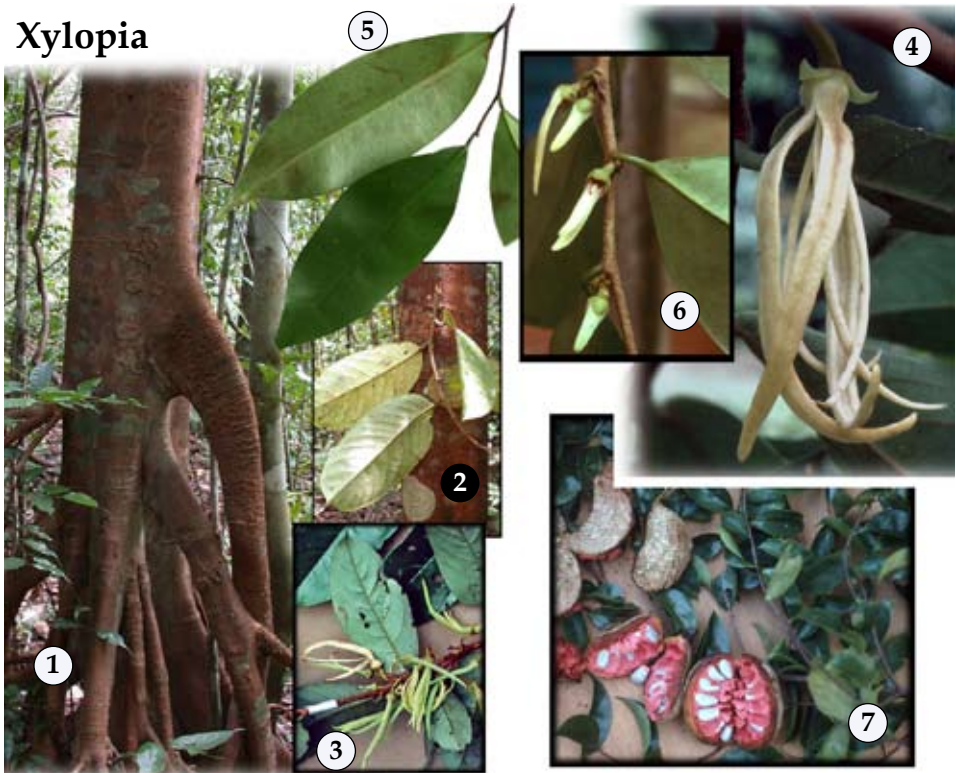
Most species seem to be shrubs found in the full sun of mountains or exposed slopes. (Not illustrated.)

GONIOTHALAMUS. [Greek, angled receptacle.]

100 species, taxonomically difficult with many poorly known species, distributed from India and Sri Lanka to New Guinea and the Philippines. This is one of the most species-rich genera in our region although usually we find only a few species in any given place. The genus is singular among Asian Annonaceae on account of the distinctive growth habit. The trees take one of two forms, either arching small trees with leaves all in a plane, or medium upright trees. The leaves of all axes are arranged in a strict distichy. The smaller trees form a curious frond in the understory of most lowland and lower hill forests. Leaves can be coriaceous or membranous, the nerves prominent, oblique, straight and parallel, and many species dry with a pimpled parchment texture.

Flowers are axillary, and many are ramiflorous or cauliflorous. The sepals number three, valvate, large or small, free or forming a cup, often persistent in fruit. The petals are six, valvate in two whorls, the outer flat or nearly so, one-veined, slightly clawed at the base; inner petals much shorter than outer, half as long or less, coriaceous, usually cohering to form a vaulted cap over the

Xylopia



Xylopia. 1, characteristic prop roots of the wet-ground species, *X. ferruginea*, Malaya; 2-4, *X. oxyantha* is similar to *X. ferruginea*, differs from many *Xylopia* in the strong regular nerves; 5-6, the typical *Xylopia* leaf with fine even venation, and 3-sided flower bud, here *X. malayana*; 7, the fruit of *X. fusca*, Malaya, are unusual in being dehiscent, exposing the red flesh and, here, immature seeds.

stamens, sometimes clawed as a pollen chamber. The stamens are many, linear-oblong, connectives apiculate or convex (that difference bears an inexact correspondence to the leaves with or without strong nerves); anther cells often transversely septate (as in *Xylopia*). The mature carpels stalked or sessile, globose or more often elongated cylindrical bearing 1 or two seeds (?four). Many species are illustrated with photographs in a review of Thai species by Saunders and Chalermglin¹¹.

Perhaps because of the distinctive vegetative form, the genus is sometimes distinguished with special names: in Borneo *hujan panas* and *lim panas*, especially for the small arching trees, and *selukai* for the larger trees. Some species are considered a mosquito repellents. In Malaya, the bark is reputedly mixed with *Eurycoma* (Simaroubaceae) in the more traditional forms of that medicine or tonic called *tongkat-ali*. Such uses only hint at the chemical richness of the genus, most of it unexplored.

XYLOPIA. [Linnaean abbreviation from the Greek for bitter-wood.] A large genus, and the only Annonaceae genus shared among Asia, Africa, and America, with a worldwide richness of about 160 species, maybe 26 species in Asia. Whether or not these can be divided into continent-exclusive clades is not yet known.

Trees and shrubs with simple hairs. The majority of the species have relatively small elliptic leaf blades (3–5 cm long) with the nervation much suppressed, reticulate and almost even with the lower surface. However the widespread *X. ferruginea* has prominent arching nerves. The first type is often called *ako* or *akau*; the second type is *jangkang*.

The flower buds are strongly three-sided; the flowers with three valvate sepals, six petals in two whorls, the outer whorl usually a little larger, spoon-shaped, weakly



A small arching tree from Lambir, Sarawak, with a type of fruit unique among Asian Annonaceae, in which the individual carpels are closely spaced and short-stalked. Each bears a single seed with a circumferential scar.

spreading but inner petals erect and touching; anther cells transversely septate with large pollen grains; ovaries one or more, style filiform with a variably broadened stigma, ripe carpels variably elongated bearing several seeds, sometimes dehiscent, but many species are not well known and the occurrence of dehiscence is poorly documented. Floral heating in association with beetle pollination was demonstrated in Sri Lanka, as cited in the family introduction. Many *Xylopia* species seem to prefer wet forests, and a few are frequent in late secondary forests. Many are rarely collected species, and more than a few still unnamed.

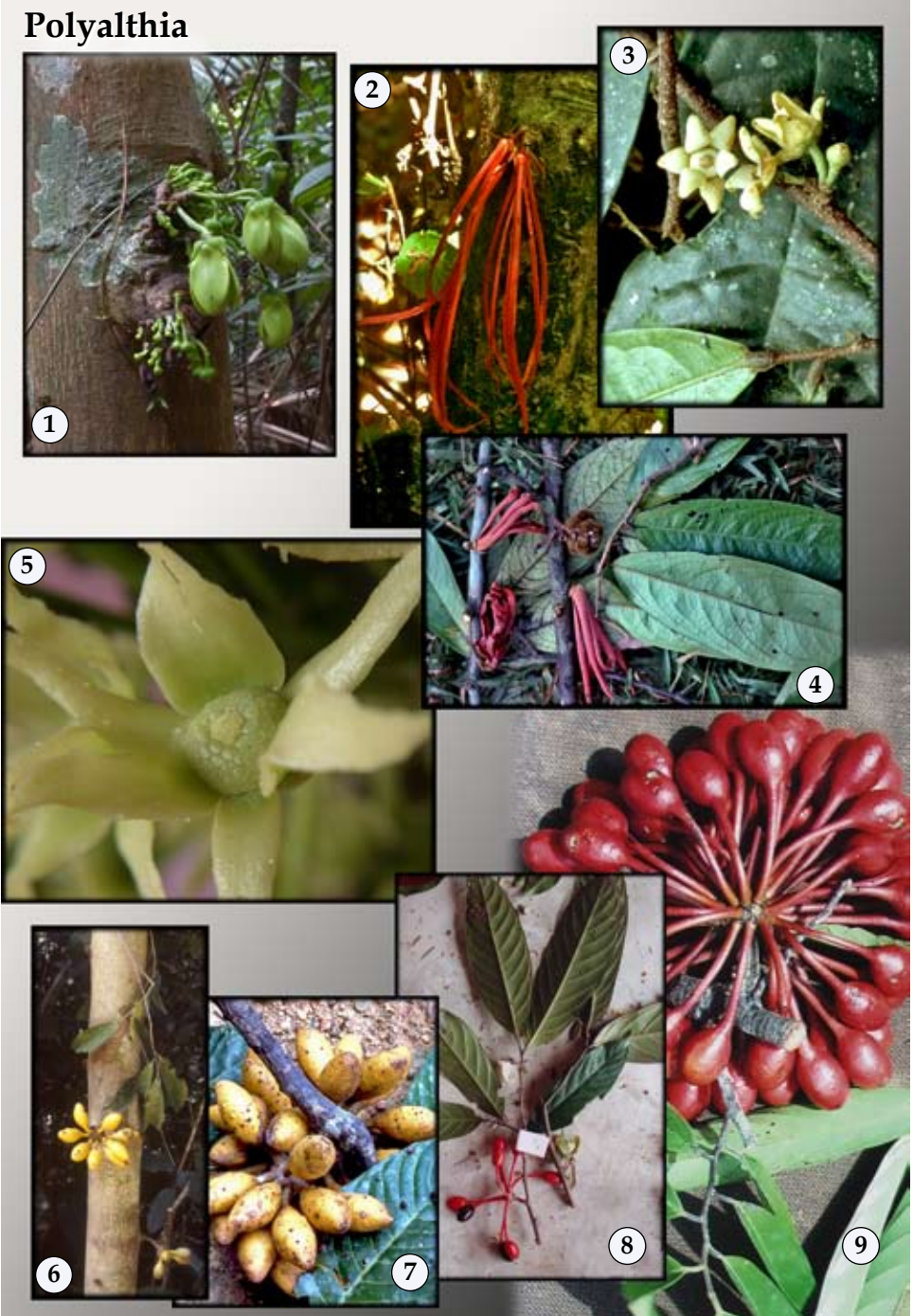
ANNONA. [From a Brazilian name.] A genus of Neotropical trees and lianas, perhaps 110 species, several of which are widely cultivated in the tropics for the fruit. Two are very common everywhere in Asia: *cherimoya* or *atis*, or custard-apple is *Annona squamosa*, and *guayabano* or sour-sop is *A. muricata*. At least *A. squamosa* is naturalized near human settlements in the Philippines. The fruit of these Neotropical plants are entirely different from the Asian

¹¹Saunders, R, et al. 2008. Botanical Journal of the Linnean Society. 156: 355–384.



Cultivated fruit from the Neotropical species of *Annona*; on the left is *A. muricata*; on the right is *A. squamosa*; both from a market in Borneo.

Polyalthia



Polyalthia, a polyphyletic genus, illustrations of the heterogeneity; 1, cauliflorous with thick green petals, *P. macropoda*, Singapore; 2, cauliflorous with long red petals, a wet-ground species, *P. stenopetala* at Pasoh, Malaya; 3, *P. obliqua*, Malaya, the flower petals short, thick and broad, the leaf base asymmetrically eared; 4, *P. cinnamomea*, Malaya, the nerves irregular, the flowers with long red petals, fruit densely hairy; 5, the flower of the cultivated *P. longifolia*; 6-7, forms of the abundant *P. lateriflora*, in fruit in Malaya, with large thick yellow monocarps; 8, an unnamed species from Sarawak, but representing a form often wrongly lumped under *P. lateriflora*; 9, a typical fruit of *Polyalthia*, here from an unnamed species from Sarawak.

Polyalthia



Polyalthia insignis, Borneo, an example of an unusual type of *Polyalthia*, single-stemmed, pachycaul, with a spiral cluster of large nearly sessile leaves, flowers borne axillary in the cluster.



Now merged in a broad *Polyalthia*, this common tree with peculiar leaf venation was formerly and widely treated as *Haplostichanthus lanceolatus* of the Philippines (© Leonardo L. Co).

Annonaceae in that the carpels are more or less completely fused.

UNPLACED. A species at Lambir Hills in Sarawak, new to science and without a name, is remarkable among Asian Annonaceae in that the infructescence consists of closely packed monocarps, flat-topped with nearly hexagonal sides and vivid purple at maturity. It has the superficial appearance of *Duguetia* or similar Neotropical genera, but note that here the carpels remain free, never fused. Floral details are lacking, as are notes on the leaf arrangement. It might as easily fall in within the polyphyletic *Polyalthia* group.

☞ - Annonaceae Short-Branch Clade - ☞☞

A difficult group of numerous genera, each defined by a combination of floral details, each feature overlapping with other genera. Thus, the distinctive features such as the Miliusoid stamens and the mitre-form petals are not synapomorphies, nor even diagnostic for a genus.

POLYALTHIA. [Greek, many-cures, in reference to reputed medicinal properties.] *Polyalthia* is the most species-rich and abundant of Asian Annonaceae genera, 100 species, distributed from Madagascar to India, S China to Australia. It is widely heterogeneous in details of form; molecular evidence decidedly demonstrates polyphyly. The variation in leaf form is so great that it

overlaps with most other Annonaceae genera. The general form of the flower includes three small sepals and six spreading petals of roughly equal length. The connective of the stamens is flat to slightly convex and there is no style; the seed bears a circumferential groove. The resolution of *Polyalthia* into natural clades is perhaps the most pressing of taxonomic issues among Asian Annonaceae.

The following paragraphs notes some of the different types of trees under this abundant genus. It is not meant to be even so much as an informal grouping, since the relationships are still poorly known.

Some species were formerly segregated under *Haplostichanthus* and *Papualthia*, differing from *Polyalthia* only in a modest fusion of the petals. We might also note that a large number of Philippine species were recently lumped all within a broadly defined *Polyalthia* [*Haplostichanthus*] *lanceolata*. They are common and abundant trees of wet and dry seasonal forests, variable in form across the Philippine Islands.

Polyalthia rumphii and *P. jenkinsii* form a pair of sister-species of the Sundaic Region, abundant in lowland forests, evidently close to *Enicosanthum*, and distinguished by the resinous patches on the large broad petals.

Polyalthia lateriflora and *P. sclerophylla*, each comprising a range of variant and ecologically segregated types; they too may join *Enicosanthum*, or be better segregated as a distinct genus.

Polyalthia insignis is a remarkable small tree, unusual in the pachycaul *schopfbau* habit, with a spiral rosette of leaves and axillary flowers.



One of the most widely and abundantly cultivated trees in tropical Asia, *Polyalthia longifolia*, originally from India, instantly recognized by the long hanging branches and tall narrow form. Too often planted singly, here growing as an effective green wall.



Polyalthia cauliflora, a misnomer since most forms of this widespread tree are not cauliflorous; the leaf blade is small, elliptic, with nerves looped well within the margin, here a dry specimen from Sarawak.



Polyalthia suberosa, Philippines, secondary forest, the flowers in this population appear to never fully mature, and yet always with fruit.

Polyalthia littoralis of strongly dry seasonal parts of tropical Asia, appeared as a strongly supported sister species to *Marsypopetalum* in the cited molecular studies. Nothing about the tree would suggest the eccentric placement.

Polyalthia longifolia is native to India, planted everywhere in tropical Asia on account of the peculiar habit wherein the branches hang close the central trunk. The peculiar habit is shared with a few native forest species such as the Bornean form of *P. bullata*.

Polyalthia suberosa is a common species of strongly dry-seasonal lands, with thick ridged, nearly winged, black bark, seemingly fire resistant. It is one of the few Annonaceae that can become common in degraded secondary forests.

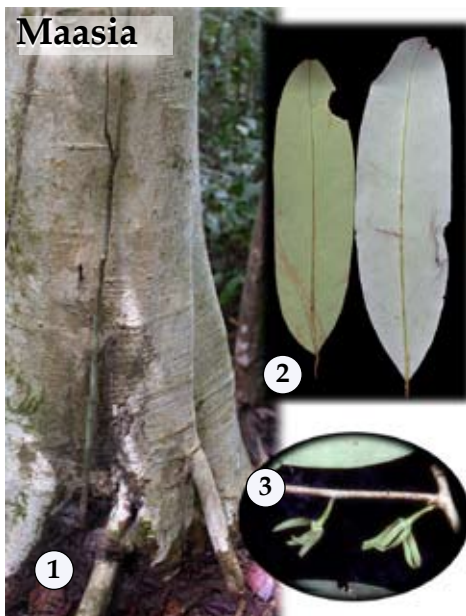
Polyalthia stenopetala is a distinctive cauliflorous species from swampy ground in Malaya, the petals very long, pendent and red. Similar flowers are found in *P. cinnamomea*, named for the densely rusty-red pubescent monocarps, which are likewise unusual in the genus.

Polyalthia cauliflora is a widespread and common species of the Sundaic Region, with small leaves and rectangular blocked nerves. Most forms are not cauliflorous but rather bear flowers and fruit among the branches.

MAASIA. [Honors of PJ Maas, authority on the Annonaceae.] A new genus recently carved out of *Polyalthia*, with six closely related species that share a more or less glaucous lower leaf surface and faint to obscure nervation. Twenty years ago, Stephen Rogstad worked at Pasoh Forest in Malaya and demonstrated co-existence through ecological specialization and habitat segregation of *P. glauca*, *P. hypoleuca* and *P. sumatrana*¹².

ENICOSANTHUM. [Latin and Greek hybrid word that presumably implies a reduced flower.] The genus *Enicosanthum* was first noted with Beccari's Bornean species, *E. paradoxum*. It now includes about 20

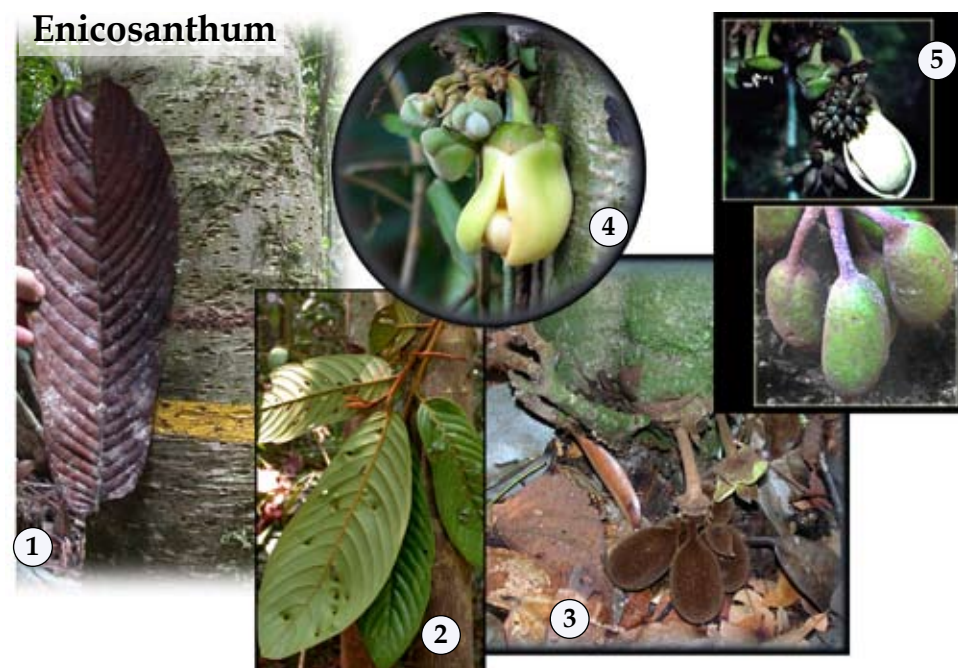
¹²Rogstad, S. 1994. American Journal of Botany. 81: 145-154.



Maasia. 1, some species, such as *M. sumatrana*, have a bright white bark; 2, comparison of the leaves of *M. glauca* (left) with *M. sumatrana* (right), both with relatively obscure nervation; 3, the flowers of *M. glauca*. All photographs from Pasoh, Malaya.



Dendrokingstonia nervosa, Pasoh, Malaya; left, the trunk; right, the fallen leaves, dried red with strong regular closely spaced nerves; above right, split and dried monocarps from a herbarium voucher, showing the several seeds.



Enicosanthum. 1, *E. coriaceum*, Sarawak, showing the large leaf, pocked gray trunk and cauliflorous inflorescence; 2, *E. fuscum*, Malaya, with a tight even golden tomentum; 3, a species at Lambir Hills in Sarawak, probably new, called *E. grandifolium* because of the similar leaves, but uncharacteristically bears densely tomentose fruit near the ground; 4-5, *E. grandifolium* from Palanan, Philippines, the flower thick and fleshy, with a musky odor and usually with small beetles within. (4-5, © Leonardo L. Co).

species, many are common and widespread in the Sundaic Region, especially Borneo, with four or five reaching the Philippines. Many species of *Encisanthum* bear large leaves with strong regular nerves and a conspicuous pubescence on the lower leaf surface, on the petals, and sometimes the fruit. More than a few are cauliflorous, each carpel with a single large seed. Formerly, *Encisanthum* was distinguished from *Polyalthia* by the imbricate sepals and petals, and the long narrow stamens. The several species are evidently related to one another, but molecular evidence also indicates that several species currently in *Polyalthia* section *Monoon*, that is, those with a with a single basal ovule, such as *P. lateriflora* and *P. scleraphylla*, are embedded within.

DENDROKINGSTONIA. [Commemorates R. Kingston, d. 1912, collector and assistant at Kew Herbarium.] Monotypic, *Dendrokingstonia nervosa*, somewhat isolated and of uncertain relationships. In flower, it is similar to *Encisanthum*, differing in the more numerous ovules and a mature fruit with several seeds in two rows. Restricted in distribution to Malaya, but widespread there at low density.

TRIVALVARIA. [Latin, three-valve, reference to the petals.] A small genus of perhaps five species, Myanmar, Thailand, Malaya, Java, Borneo and Sumatra. Generally similar to *Polyalthia*, but shares with *Encisanthum* overlapping floral parts. It differs from the latter in the flowers of mixed sexuality (unconfirmed in the field) and the inflorescence nearly sessile and extra-axillary. *Encisanthum* bears bisexual flowers on stalked inflorescences that are either axillary or cauliflorous. The leaves of *Trivalvaria* are weakly recognizable: the nerves decurrent on upper surface where they join the midrib, the upper mid-

Trivalvaria



Trivalvaria, from Pasoh, Malaya. 1, *T. macrophylla*, juvenile, 2 cm DBH, leaf blade with regular nerves arched to the margin, scalariform venation; 2 & 3, *T. pumila*, flower, 8 mm wide, flower and young fruit, spotted.

rib slightly wrinkled, the veins more or less scalariform at right angle to the midrib. Molecular evidence (only *T. macrophylla*) weakly allied the species with a poorly supported group of *Polyalthia*. These are all small trees, in the case of *T. pumila*, rarely more than one m tall.

MEIOGYNE. [Greek, small-gynoecium.] A genus of about 24 species of small trees distributed throughout tropical Asia from India to the Philippines. *Meiogyne*



Meiogyne. 1-2, *M. monosperma*, 1, leaf and flower from Malaya; 2, a specimen of dried leaves from Sarawak, the main nerves looped well within the margin, the blade dries red in color; 3, *M. virgata*, specimen of the dry leaf from Sarawak, note the strong regular nerves and wrinkled papery blade; 4-5, *M. cylindrocarpa*, Sarawak, with fine, nearly dryobalanoid nervation.

Miliusa



Miliusa - *Saccopetalum* type. Unlike the small shrubs that comprise most species of *Miliusa*, these are large trees, among the largest in the family, and generally found only in the strongly dry-seasonal parts of Asia. 1-3, *M. lineata*, Huai Kha Khaeng, Thailand; 1, mature tree with fluted bole and shaggy bark; 2, fruit and leaf; 3, flower; 4-7, *M. vidalii*, Mt. Makiling, Philippines; 4, mature tree in flower, note the flower pendent from a 15 cm long stalk; 5-6, note the deep saccate petals and the color change in the petals as the flower matures; 7, leaves. (Photograph 3, © Sarayudh Bunyavejchewin.)

differs from *Polyalthia* in that it bears three-five seeds per monocarp instead of one, and in the sessile, discoid stigma. Especially in the type species, *M. virgata*, the petals are odd in that they bear a rough warty patch on the inner face near the base. *Meiogyne* now includes the genera *Oncodistigma*, *Cheimodendron*, and *Polyaulax*. Thus, one of the most abundant species is now *Meiogyne* [*Oncodistigma*] *monosperma*, which differs notably from the others in that nerves of the leaf blade are strongly looped and boxed. Also note that the specific epithet is a misnomer in that the seeds number one-four.

MILIUSA. [Commemorates Baron PB de Milius, d. 1829, accompanied Leschenault on the Baudin Expedition.] About 40 species from India and Sri Lanka throughout tropical Asia to Australia. The genus is distinguished by the flowers which are solitary or in clusters of two or three, on slender stalks, axillary, the perianth in three whorl of three, each whorl valvate, the outer six roughly equal and small (usually interpreted as three sepals and three outer petals) while the three inner petals are long, thickened, fleshy, cup-shaped at the base in the species illustrated (but not so in all species), cohering at their edges at first, later free; the anther connective is without prolonged apex; the stigma globose or elongated club-shaped.

The name *Saccopetalum*, which emphasizes the deeply saccate petals, was formerly used to draw a distinction for a few species of large canopy trees, abundant in strongly dry seasonal lands. These species were thought to be further distinguished by the more numerous ovules. Sinclair, among others, found the differences indecisive. In Mainland SE Asia we find a very large tree with a shaggy black bark and deeply fluted bole; it is common and abundant in lowland evergreen and mixed deciduous forests, and was the most abundant tree in the 50-ha plot in Huai Kha Khaeng, Thailand. It is well known to foresters as *Saccopetalum lineatum*, and while that name is now synonymized under *Miliusa lineata*, note that this is not the tree described in GARDNER *loc. cit.* as a shrub three m tall. A similar large tree of the Philippines is *Miliusa* [*Saccopetalum*] *vidalii*, where the flowers are pendent from exceedingly long stalks, 10-15 cm in length. Two other similar species are *M. horsfieldii* of Sumatra and *M. arborea* in the Philippines. The rest of the genus *Miliusa* comprises smaller trees, the largest of which might be *M. velutina*, illustrated in GARDNER *loc. cit.*; note the petals in this species are not saccate at all.

OROPHEA. [Greek, ceiling, in reference to the vaulted ceiling of the three inner petals.] 41 species from India throughout tropical Asia. These are all small understory trees, usually no more than two-four cm DBH.

Orophea



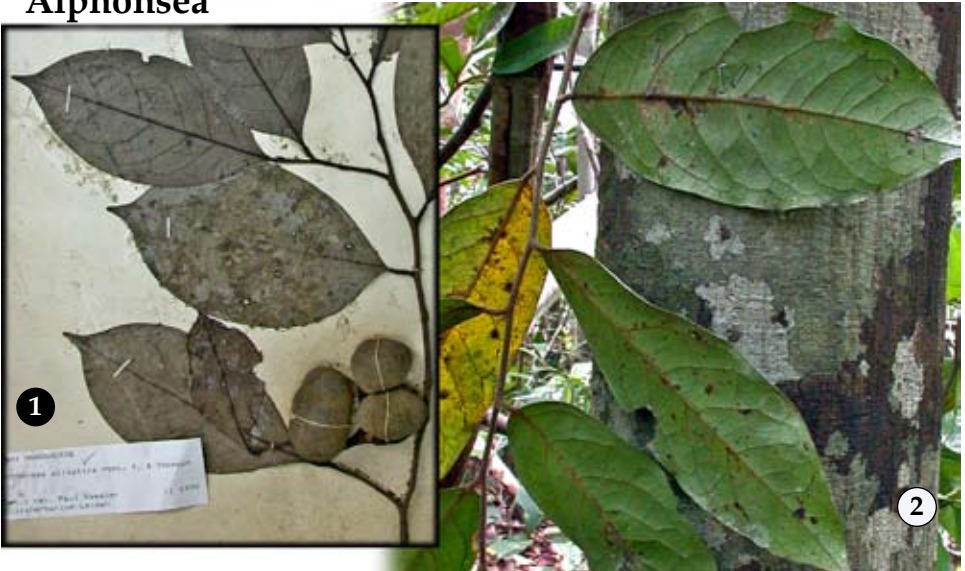
Orophea. 1-2, a species typical of the genus, but possibly undescribed, from Pasoh, Malaya, the flowers discolored from alcohol; 3, line illustration and floral diagram from BALLION *loc. cit.*

Among the many species the flower is fairly uniform and recognizable: three small valvate sepals and six valvate petals, the outer three larger than the sepals and petaloid, while the inner three vaulted and mitriform. The stamens number six to 12. Two types of carpels—the globose as in *O. polycarpa*, and elongated string-of-pearls as

in *O. hexandra*. Many of the individual species closely resemble each other.

ALPHONSEA. [Commemorates Alphonse de Candolle, d. 1893.] About 25 (or 40) narrowly distributed and poorly known species scattered throughout tropical Asia. (It may occur in the Philippines, but not yet recorded there.) In most species the leaves are leathery, shining, glabrous or hairy, the margin is often inrolled. The flowers are poorly known, and only from a few species (see the illustration in GARDNER *loc. cit.* of *Alphonsea boniana*). The three sepals are several times smaller than the six petals which are in two series, each with slightly saccate base and reflexed tip; the outer petals fully reflexed and the inner are joined to form a cone with reflexed tips. The fruits vary from nearly sessile to stalked, thick walled, glabrous, hairy or warty. More than most any other genus of Annonaceae, the species of *Alphonsea* are poorly known, often from little more than the type collections. It may be paraphyletic with respect to *Platymitra*. The genus includes a few species of the lower canopy trees, but also small multi-branched trees of the understory. One of the few genera to be encountered at elevations over 1000 m.

Alphonsea



Alphonsea. 1, herbarium specimen of *A. elliptica*, with characteristic leaf and fruit; 2, *A. maingayi*, leaf and trunk from Pasoh, the thin black bark has a strong celery odor when cut.

Phaeanthus



Phaeanthus ophthalmicus, from Malaya, the leaf dries black, papery, with scalariform venation; leaf and fruit on long pendent stalk; flower.

PLATYMITRA. [Greek, flat-mitre, reference to the shape of the petals.] These are tall trees with glabrous leaves bearing faint nerves. The flowers are small and ramiflorous, the petals are thought to be similar to *Orophea*, that is, with the three inner petals in mitre-form arrangement, but the study of fresh and developing flowers is wanting. The genus may be nested within *Alphonsea*. Two species: *Platymitra siamensis* is an abundant and important tree of mid montane evergreen forests in Mainland SE Asia, and the widespread *Platymitra arborea*, not in the lowland Sundaic forests, but often abundant in evergreen forests of the surrounding region of Thailand, Sumatra, Java and the Philippines.

PHAEANTHUS.

[Greek, dusky-colored flowers.] A relatively distinctive genus of maybe 12 species from S India and Myanmar east to Cambodia and south through the Malay Peninsula to Borneo, New Guinea and the Philippines. These are small trees with extra-axillary flowers consisting of three valvate sepals, three very small outer petals like a second whorl of sepals, and three large fleshy inner petals in mitriform arrangement. The stamens connectives are flat-topped, not concealing the pollen sacs; the cylindrical ovaries bear a distinct style and elongated club-shaped stigma, one-seeded. Most species are quickly recognized to genus by the thin, papery leaves that dry black and bear strong regular nerves with even scalariform venation. (In New Guinea, the leaves of *P. macropodus* bear a more lax reticulate venation, sometimes only patches of black.)

Marsypopetalum



Marsypopetalum pallidum, a sterile voucher from Lambir, Sarawak, with diagnostic venation, and purple twig.

MARSYPOPETALUM.

[Greek, pouched petal.] Treated as the monotypic *M. pallidum*, originally described from Java, widespread in Borneo, rarely collected in Johore, and with a distinct form in Malacca. Small tree, simple hairs, flower supra-axillary, sepals three, valvate, petals six, valvate, in two whorls, outer much shorter than inner, concave at base, connective with a truncated dilated apex. The monocarps are oblong and stipitate. When dry, the purple twigs and bright green leaves, thick, billowed with looped nerves are distinctive. The molecular studies cited showed a linkage with *Polyalthia littoralis* that was surprisingly strong, although the pair fall without resolution within the weakly resolved short-branch clade.

SAGERAEA.

[From an Indian name.] Maybe nine species, all very similar, from the Indian Peninsula, Sri Lanka, Myanmar to Malay Archipelago and Philippines. The main difference with the broad *Polyalthia* lies in the numerous ovules which number six-eight in two rows. *Sageraea elliptica* is commonly encountered in the Sundaic Region. The leaf is large, thick and dries deep red, superficially similar to some species of *Diospyros*, but note here the midrib sunken above, the peeling bark of the twig and reticulate fibers within. A similar tree that is exceedingly common in the lowland forest of southern Vietnam goes by the same name, but it is doubtfully identical.

STELECHOCARPUS.

A genus of five or six species, Mainland SE Asia, Malaya, Java to New Guinea.

Curiously differs from most other Annonaceae trees in Asia in the strongly raised midrib of the upper leaf surface (some lianas and many American species have a raised midrib). The illustrated species bears flowers at the base of the trunk on stalks no more than three cm in length, and is named *Stelechocarpus cauliflorus* following Sinclair. However, the digital images of an isotype at Leiden, taken from a tree cultivated in Bogor and sourced in Sumatra, shows a floral cluster cut from the tree in which each flower is subtended by a 5-10 cm long stalk. *Sageraea burahol* is the edible *keppel* fruit, said to make the body and its excretions smell of violets. Molecular studies sampled both of these species and found them unrelated; however, *S. burahol* was wrongly described as Central American, so some question remains as to the accuracy of the sample. The morphology is singular and concordant and certainly implies a strong clade.

MITREPHORA. [Greek, mitre-bearing, reference to the mitre-shaped form of the three inner petals that arch over the receptacle.] Currently treated as 48 species from India and Sri Lanka to S China eastward to the Philippines and Australia with at least a few species fairly common and abundant in most of tropical Asia. These vary from small understory trees to larger trees of the lower canopy. The leaves tend to have strong regular evenly spaced nerves and fine reticulations; the blade

shape is often ovate-elliptic with very clean neat margins. It appears to be unique in bearing rhomboid calcium-oxalate crystals in the leaf epidermis above the main nerves (See the photographs in the study by Weerasooriya and Saunders¹³.)

The flowers of *Mitrephora* are bisexual, extra-axillary and typically with several flowers in a cymose inflorescence; the outer petals are equal to or larger than the inner mitriform petals. *Pseuduvaria* is segregated because the flowers are often unisexual, single and axillary, and the outer petal whorl is sometimes shorter than the inner mitriform petals.

The study of Indochinese species cited above usefully corrects the misapplication of the Malayan *M. maingayi* to specimens from the mainland, while the important tree of mainland evergreen forests widely cited under the name *M. thorelii* should properly be *M. tomentosa*.

PSEUDUVARIA. [Greek, close to *Uvaria*.] A genus comprising 52 species from Myanmar to northern Australia, chiefly centered in New Guinea (20 species) but with a few species everywhere. The genus was recently monographed¹⁴. The leaves of *Pseuduvaria* are relatively uniform, being thin papery, with numerous very regular and very straight nerves. Most species are small understory trees, similar to *Mitrephora* but with single axillary flowers, often unisexual (dioecious), with inner petals usually longer than outer petals. At least in some species the inner petals are dark purple or red and bear special-

¹³Weerasooriya, A, *et al.* 2005. Systematic Botany. 30: 248–262.

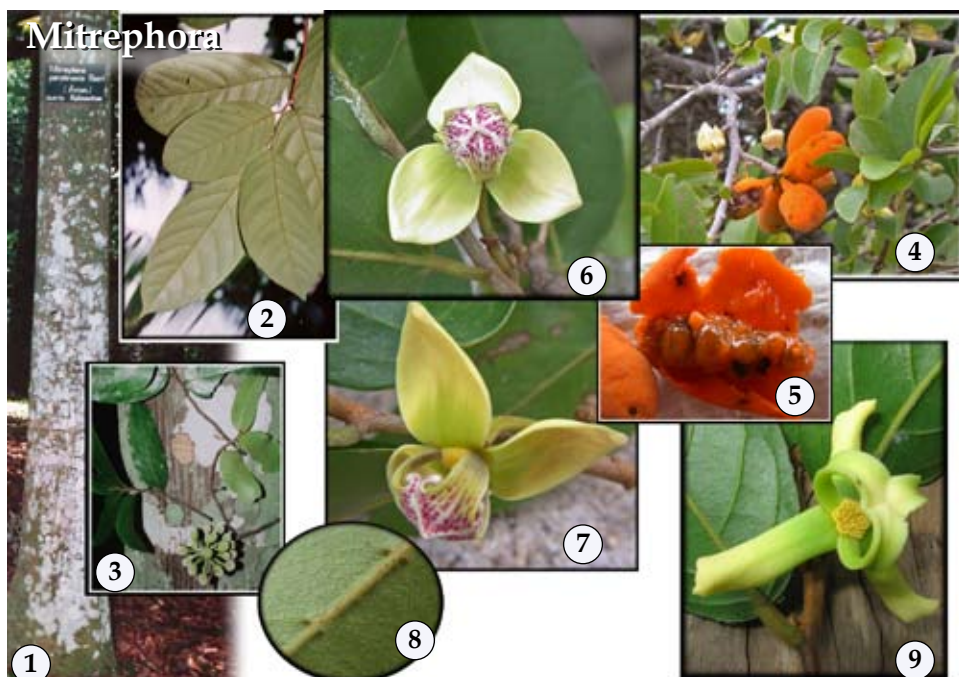
¹⁴Su, Y, *et al.* 2006. Systematic Botany Monographs. 79: 1-204.



Sageraea elliptica, herbarium specimen from Pasoh; the blade is thick and hard, shiny red below, venation distinctive.



Stelechocarpus cauliflorus, Malaya, the flowers upon swollen growths from the base of the tree, the leaf blade with the midrib strongly raised above.



Mitrephora. 1-2, *M. polypyrena* from Java, here cultivated in the Bogor Botanic Garden; 3, the similar *M. tomentosa* (= *M. thorelii*) in Thailand, with hairy leaves and fruit; 4-8, a small multi-branched shrub in Nui Chua National Park, Thailand, *M. pallens*; 4-5, the mature fruits fall apart revealing the numerous slippery flesh-covered seeds; 6-7, the floral form typical of the genus, day-blooming with violet patches in the inner petals suggests fly-pollination; 8, unusual in the Annonaceae in the fine, even and nearly obscure venation, and the strong pit domatia at the axil of the major nerves; 9, an unidentified species of *Mitrephora* from Palau, Philippines, with strapped-shaped petals. (Photograph 9, © Ulysses Ferreras.)



Pseuduvaria macrophylla, Malaya, elliptic, thin softly hairy leaves with many strong regular nerves; the flower about 6 mm across.



Neuvaria acuminatissima, a voucher specimen from Sarawak with a single fruit; the leaf showing the strong regular nerves, the stellate hairs and pimpled texture, similar to *Popowia*.

ized dark red glands on the abaxial face; the flowers emit a fetid odor, and the flowers are fly-pollinated.

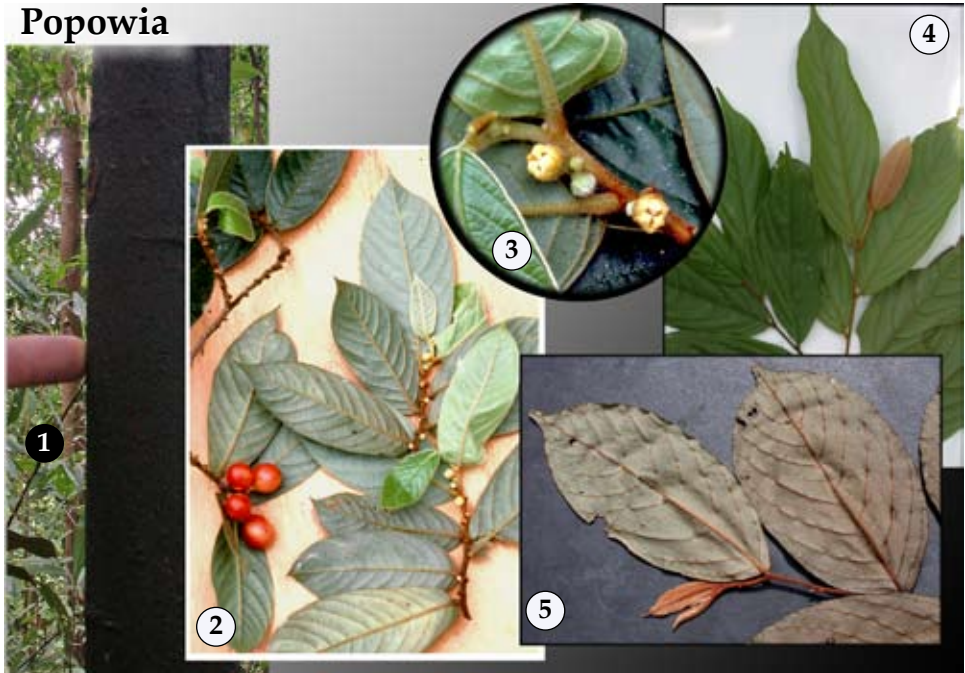
NEOUVARIA. [Greek, close to *Uvaria*.] Four species, Peninsular Thailand, Sundaic Region and the Philippines. Initially striking in the characteristic stellate hairs on twigs and leaves; flowers unisexual; mitriform; stamens 20-30, very short with broad, convex, truncate connectives. Ovaries four to 12, oblong-ovoid, pubescent, the stigma clavate, glabrous, bent outwards slightly, ovules one-two. The monocarps number one-six; they are hard, slightly hairy, nearly sessile and bear a single seed. Despite the name, the only resemblance to *Uvaria* is that both have stellate hairs. With *Popowia*, the genus shares a leaf texture, indumentum, and inner petals with concave bases.

POPOWIA. [Commemorates J. Popowitch, d. 1774, Professor of Botany, Vienna.] About 30 species, about ten in tropical Asia, S India to Australia, and at least *P. pisocarpa* north to central Luzon. The type species of *Popowia* as well as many others are recognized in Africa

and Madagascar; their relationship to the Asian species needs to be confirmed. *Popowia*, or at least the Asian representatives, share many features with *Pseuduvaria*, *Mitrephora* and *Neouvaria*. All four genera have similar stamens with flat-topped connectives.

All of our species are small trees. The leaves are peculiar and recognizable in that they dry with a characteristic pimply texture. Some species are sparsely hairy while others are densely stellate hairy. The flowers are small, among the smallest of all our Annonaceae. A few opposite the leaves, three valvate sepals; three outer petals small, spreading sepal-like + three inner petals, larger concave inside, sometimes with fused base; stamens with broad, flat-topped or slightly concave connectives; ovaries few, ovoid to oblong, style very short, stigma grooved on the top; monocarps globose with short stalk with one to four pitted seeds with a circumferential ridge. The flowers are among the smallest of Annonaceae flowers, and thrips have been reported to be an effective pollinator (see citation in the family Overview).

Two species, *P. pisocarpa* and also *P. tomentosa* are especially abundant and widespread in forests of the lowland Sundaic Region.



Popowia. 1-3, *P. tomentosa*, a small tree with black bark, the flowers only 4 mm across; 4-5, *P. pisocarpa*, fresh and dried leaves showing the red color of new foliage and the distinctive texture when dry.